RADIAL GROWTH PATTERNS OF JACK PINE IN RELATION TO CLIMATE, MOISTURE AVAILABILITY, AND DWARF MISTLETOE INFECTION IN THE BOREAL PLAINS ECOZONE OF SASKATCHEWAN, CANADA

A Thesis Submitted to the College of

Graduate Studies and Research

In Partial Fulfillment of the Requirements

For the Degree of Master of Science

In the Department of Biology

University of Saskatchewan

Saskatoon

By

MEGAN HORACHEK

PERMISSION TO USE

In presenting this thesis in partial fulfilment of the requirements for a Postgraduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professor or professors who supervised my thesis work or, in their absence, by the Head of the Department or the Dean of the College in which my thesis work was done. It is understood that any copying or publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

Requests for permission to copy or to make other use of material in this thesis in whole or part should be addressed to:

Head of the Department of Biology
University of Saskatchewan
Saskatoon, Saskatchewan S7N 5E2

ABSTRACT

Drought stress is increasing as a result of climate change, and is thought to be driving episodes of tree mortality that have been observed in every forested region on Earth. In the western boreal forest, potential interactions between drought stress and forest diseases could lead to forest fragmentation and range contractions. Lodgepole pine dwarf mistletoe (*Arceuthobium americanum*) (DM) is a host specific, parasitic plant of jack pine (*Pinus banksiana*) that affects resource allocation, water use, and growth. Despite being one of the most damaging pests to jack pine in the Canadian boreal forest, it has not been well studied in relation to the potential impacts of climate change. I used tree ring and climate data to investigate growth-climate responses of jack pine in infected and uninfected stands, across the regional moisture gradient associated with the boundary of the boreal forest in southern Saskatchewan. I sampled across three study regions extending from remnant island forests in the drier Aspen Parkland Ecoregion, to the wetter interior of the mid-boreal upland and boreal transition ecoregions within the Boreal Plains Ecozone (BPE). Radial growth was negatively impacted by DM infection across all study regions. Severely infected trees showed a divergence in radial growth from healthy trees, with few exceptions. Ring-width correlation with summer temperature was altered in infected trees. Infected trees at the southern boundary of the boreal forest showed the greatest change in climate response, as the positive relationship with moisture variables (spring precipitation and spring Climate Moisture Index), seen in healthy trees, collapsed to zero or became marginally negative when trees were infected. This result and the decline in radial growth suggest that DM has an impact on trees growing in the southern BPE of Saskatchewan. This could lead to a contraction of the boreal forest as extensive mortality of infected jack pine could occur at its southern range limits. Jack pine is a commercially and ecologically valuable species in the boreal forest and understanding its potential responses to climate change will be important for the future sustainable use of forest resources.

ACKNOWLEDGMENTS

First of all, thank you to my supervisor Jill Johnstone for giving me this opportunity, for the guidance in those early weeks when I was lost and confused, and the support when I decided to change my focus to dwarf mistletoe. To my co-supervisor, Colin Laroque, big thanks for the extraordinary support, over the past year in particular, for guiding me in the world of dendrochronology, and for all of those trees cored. It has been a pleasure working with you both, and I am grateful for the experience. I would also like to thank my committee members Dan Pennock, Jeff Lane, and Ted Hogg, for taking the time to help and advise me over the past 2 years.

I need to acknowledge the assistance of my fellow MAD-Labbers in the lab and field, without whom I am unsure how I would have cored all 360 of those trees (twice). Thanks to Nicole Marleau for accompanying me on so many trips, for the good company, and for digging so many soil 'pits'. Thanks also to Jay Maillet, Scott Wood, Owen Laroque, and Magali Furlan Nehemy for all of your help in the field. I would also like to thank my fellow NPEL-er's, past and present. Thanks in particular to Ruth Greuel, Alix Conway, Mélanie Jean, and Alexandre Truchon-Savard for your help and support in this final stretch – Cheers! To Xanthe Walker and Steve Mamet, thank you so much for the R-code and teaching me the ways of tree-ring research.

Finally, thank you to the Changing Cold Regions Network for financial support, and to the Global Institute for Water Security for the use of field trucks, to the Biology Department staff for all of their assistance.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

ABBREVIATIONS

AIC: Akaike Information Criterion

BERMS: Boreal Ecosystem Research and Monitoring Site

BP2: Jack pine/lichen ecosite, moderately fresh sand

BP3: Jack pine/ feathermoss ecosite, moderately fresh loamy sand

BPE: Boreal Plains Ecozone

CMI: Climate Moisture Index

DBH: Diameter at breast height

DM: Lodgepole pine dwarf mistletoe

EPS: Expressed Population Signal

GPS: Global Positioning System

MPB: Mountain pine beetle

MS: Mean Sensitivity

CHAPTER 1

INTRODUCTION

Tree mortality has been increasing in every forested region on the planet and the primary driver is thought to be climate change-induced drought stress in forest ecosystems (Allen et al. 2010, Williams et al. 2013). Important interactions between drought stress and disturbance processes may be exacerbating the effects of climate change on forests. The structure and function of forest ecosystems is the result of multiple interacting disturbance regimes (Weed et al. 2013) that can vary in time and space. Climate change will alter these disturbance regimes and how they interact (Weed et al. 2013). Disturbance results from either biotic or abiotic factors. Abiotic disturbances, such as fire, are well known mechanisms of change in forest ecosystems. Some biotic disturbances are well studied, such as insect pests, and others, such as dwarf mistletoes, are less well known (Weed et al. 2013). Biotic disturbances can be important mechanisms of change in forests, particularly in their interaction with changing climate. In North America, interactions between drought stress and biotic disturbance (forest pests and disease) has led to the loss of tens of millions of hectares of forest across the continent (Allen et al. 2010).

Biotic disturbances in the western Canadian boreal forest range from forest insect pests to diseases and pathogens, which lead to reduced growth or mortality in boreal forest tree species (Moody and Amirault 1992). The impacts of insect pests have been well documented in the Canadian boreal forest (Moody and Amirault 1992). Insect pests include tent caterpillar (*Malacosoma disstria*), budworms (*Choristoneura* spp.), and bark beetles (*Dendroctonus* spp. and *Ips* spp) (Moody and Amirault 1992, Volney and Fleming 2000). Tent caterpillar causes decreases in aspen (*Populus tremuloides*) growth in the Boreal Plains Ecozone (BPE) which may be exacerbated by drier climatic conditions (Hogg and Brandt 2002), as aspen is prone to dieback under drought stress alone (Hogg et al. 2008). Jack pine mortality in stands defoliated by jack pine budworm (*Choristoneura pinus*) persists for several years after an outbreak (Volney 1998). Jack pine radial growth takes several years to recover from an outbreak of two or more compounded years, after which point mortality is very high (Volney 1998). A lag in mortality of 16-24 years following a jack pine budworm outbreak compounded by drought stress in the BPE has also been documented (Mamet et al. 2015). Bark beetles, such as the mountain pine beetle (MPB) (*Dendroctonus ponderosae*), kill host trees by feeding on phloem that leads to girdling of the main stem (Safranyik and Carroll 2006). Additionally, beetles introduce a fungus, which

impedes water transport (Safranyik and Carroll 2006). Changes in climate in British Columbia have led to an increase in suitable habitat for the MPB. Furthermore, fire suppression on the landscape compounded this resulting in a vast number of mature pine forests that were susceptible to attack (Taylor et al. 2006). This combination of warmer than average winters, fire suppression, and abundance of mature habitat led to widespread mortality of lodgepole pine (*Pinus contorta*) throughout British Columbia (Carroll et al. 2003, Taylor et al. 2006).

Diseases in the boreal forest include wood decay fungi (such as the root rot fungi, *Armillaria* spp.), and dwarf mistletoes (*Arceuthobium* spp.) (Moody and Amirault 1992, Mathiasen et al. 2008). Root rot from *Armillaria* spp. infections can lead to radial growth decline, weakened roots, and mortality, and it can afflict both coniferous and deciduous hosts (Moody and Amirault 1992). Dwarf mistletoes are parasitic plants that affect a wide array of conifer species (Hawksworth and Wiens 1996). There are six species of *Arceuthobium* that infest conifers in Canada (*A. americanum*, *A. douglasii*, *A. laricis*, *A. pusillum*, *A. tsugense* ssp. *tsugense*, and *A. tsugense* ssp. *mertensianae*) (Hawksworth et al. 2002). Only two species of *Arceuthobium* occur east of British Columbia: *A. pusillum* and *A. americanum* (Hawksworth and Wiens 1996).

Lodgepole pine dwarf mistletoe (*Arceuthobium. americanum*) [Santalales: Viscaceae] (DM) is a host-specific obligate-parasitic plant that infects both lodgepole pine and jack pine in Canada. It affects resource allocation, water use, and growth form of the host tree (Hawksworth and Wiens 1996, Epp and Tardif 2004, Hiratsuka et al. 2004). The result is reduced wood quality, reduced seed production abnormal growth, a decline in tree health, and ultimately mortality (Hawksworth and Wiens 1996, McIntosh 2004, Saskatchewan Ministry of Environment 2010). The BPE is the region most affected by DM in Canada, accounting for 73% of infected jack pine forest (Brandt et al. 1998). DM is native to western Canada, and is one of the most damaging organisms to jack pine in the boreal forest (Brandt et al. 1998). Jack pine death due to mistletoe infection in the Prairie Provinces of western Canada was estimated at 1.5 million m^3 between 1994 and 1996 (Brandt et al. 1998). Despite this, damaging organisms such as DM are among the least studied biotic disturbances in the Canadian boreal forest, particularly in relation to climate change (Weed et al. 2013).

Jack pine is a dominant and commercially important conifer species of the boreal forest (Brandt et al. 2013), and has the broadest distribution of any pine species in Canada (Farrar 1995). It is known for its ability to survive in dry environments, where other dominant boreal tree

species cannot (Rudolf and Laidly 2004). Despite this, jack pine distribution in western Canada has been shown to be limited by moisture at the southern extent of its range (Hogg 1994, 1997, Brooks et al. 1998). The southern boundary of the boreal forest is vulnerable to changes in the abundance and availability of moisture and together with additional biotic and abiotic stressors even jack pine may struggle to survive under drier environmental conditions predicted under a changing climate. In order to mitigate potential future losses of jack pine to DM infection it is important to understand the impacts of DM on jack pine growth in response to changing climatic conditions in the BPE.

Increases in the frequency and severity of drought events are expected for the southern boreal forest of western Canada (Peng et al. 2011, Price et al. 2013). Projections also indicate the potential for a change in the Prairie-BPE, where a moisture deficit occurs as higher temperatures lead to an increase in evapotranspiration (Hogg 1994, 1997, Hogg and Hurdle 1995). As the dry prairie climate shifts northward into the southern reaches of the boreal forest, there may be fragmentation and range contractions of boreal species, such as jack pine (Hogg and Bernier 2005). In the southern boreal forest of western Canada, drought stress will be a key consequence of climate change, but the interaction with forest diseases, such as DM infection, is not well understood (Allen et al. 2010, Price et al. 2013).

Studies of other mistletoe species and their respective host tree associations have shown mixed responses to infection. In one case increases in radial growth of Ponderosa pine (*Pinus ponderosa*) infected with *A. americanum* were observed with an increased sensitivity to climate variables (Stanton 2007). Scott and Mathiason (2012) found that infected Bristlecone pine (*Pinus aristata*) displayed consistent reduction in radial growth in another study, and high mortality when interacting with other stressors. Yet another study illustrated an increase in sensitivity of Scots pine (*Pinus sylvestris*) to climate variability that was consistent with increased drought stress (Sangüesa-Barreda et al. 2012, 2013). In western Canada, one study found that DM had little impact on diameter at breast height (DBH) of jack pine in Manitoba, but impaired vertical growth and increased tapering of the main stem (Moody and Amirault 1992, Epp and Tardif 2004). Another study conducted in Manitoba reported a reduction in jack pine forest productivity as estimated with remote sensing (Baker 1992). Other than these examples, research on the impact of climate variability and drought stress on pines infected with dwarf mistletoes is limited, and impacts on jack pine infected with DM in Canada is still a major knowledge gap. The

physiological impact of DM on jack pine, along with the projected changes to the climate may lead to severe alterations to the southern boreal forest as we know it in western Canada.

To address the impacts of DM infection on jack pine in the boreal forest of western Canada, I aim to answer the following questions:

1) Does DM infection change the radial growth pattern of jack pine in the BPE of western Canada?

2) Does DM infection change the relationship between jack pine radial growth and climate in the BPE?

3) Is infection with DM a primary influence driving differences in the climate-radial growth relationship in infected versus healthy jack pine?

4) Does DM infection interact with the effects of drought stress experienced at the southern range limits of jack pine in western Canada?

To accomplish this I will use tree-ring analysis and a climate correlation analysis to compare healthy and infected trees across a regional moisture gradient in the BPE of Saskatchewan. If DM alters resource allocation I expect to see 1) reduced radial growth in severely infected trees as resources are directed to the infection and away from other growth processes and; 2) increased sensitivity to climate variability of infected trees as resources become more limited to the tree. If climate sensitivity is altered in infected trees I expect that DM 3) will be a primary influence driving differences in climate sensitivity for all climate variables and; 4) infection will show an interaction with study region indicating an increasing influence on infection in the driest regions.

CHAPTER 2

METHODS

2.1 Study Regions

2.1.1 Description

The BPE (Figure 2.1) climate is characterized by short summers with warm temperatures, and long cold winters (Acton et al. 1998). Temperatures increase with latitude from north to south (Acton et al. 1998). Overall precipitation in this region is low with an average annual rate of 450 mm (Johnston et al. 2008), but is variable and often greater in the summer (Acton et al. 1998). Warmer and drier conditions at the southern boundary result in a transition from boreal forest in the North to aspen parkland and prairie in the South. This transition represents a large portion of the BPE in Central Saskatchewan (Figure 2.2). There is a moisture gradient that runs from the cooler and moister northern expanses of the boreal forest to the warmer and drier southern boundary (Hogg 1994, Zha et al. 2010).

All study sites were located between La Ronge, SK in the North through to southeast of Prince Albert, SK in the south (Figure 2.3). There were nine sites in each of the three main study regions (Table 2.1): the Northern region, the BERMS (Boreal Ecosystem Research and Monitoring Site) region, and the Southern region. The Northern region was located along Highway 2, at the intersection with Highway 165 west, and along Highway 165 east, at the junction with Highway 912. The BERMS region was found near the 'Old Jack Pine' (Barr et al. 2012) site, off of Highway 106 approximately 50 km north of Smeaton, SK. The Southern region was located in the Fort à la Corne island forest, south of Highway 55, west of Highway 6, and to the north of the North Saskatchewan River approximately 60 km east of Prince Albert, SK.

The Northern and BERMS study sites were located within the Mid-Boreal Upland ecoregion, and the Southern sites in the Boreal Transition ecoregion, within the broader BPE. In the Mid-Boreal Upland ecoregion the mean summer and winter temperature ranges from 13°C to 15.5°C, and -13.5°C and -16°C, respectively (University of Saskatchewan 2006). The range of mean annual precipitation is 400 to 550 mm (University of Saskatchewan 2006). The Boreal Transition ecoregion has a mean summer temperature of 14°C and mean winter temperature of -13.5°C (University of Saskatchewan 2006). Mean annual precipitation in this ecoregion ranges from 450 to 550 mm in the west and east, respectively (University of Saskatchewan 2006). In

both ecoregions, jack pine dominated forest occurs on dry, sandy textured soils, which are often nutrient poor (Acton et al. 1998). Coarse or sandy areas in both ecoregions are dominated by Brunisolic soils, with Gleysols and Organic soils occurring in local depression and low-lying areas. The topography of these regions is similar, with gently sloping or undulating areas, but mainly level plains. In the Boreal Transition, there is additionally a hummocky appearance in sandy areas where wind has reworked the landscape. Jack pine dominated forest is limited to the dry, sandy, well or rapidly drained and more nutrient poor soils, characterized by Brunisols (Acton et al. 1998).

2.1.2 Climate data

I obtained daily climate data (current to June 2015) from Environment Canada climate stations in La Ronge, Prince Albert, and Pilger, Saskatchewan (Environment Canada 2015). These climate stations were selected based on proximity to my three study regions, were distributed from North to South and reflective of the regional climatic gradient, and provided the most complete records of temperature and precipitation (Figure 2.3). The climate station in Waskesiu, SK was excluded due to missing data. Climate stations were used in lieu of interpolated data for specific sites to ensure quality of climate data throughout the period of analysis. Individual sites were so similar in local climate that interpolated data for each was not warranted for this analysis. The daily climate data were downloaded from an Environment Canada FTP server, and provided to me by Michael Michaelian (Northern Forestry Centre) in November 2015. Daily minimum and maximum temperatures, and daily total precipitation values were imported into BioSIM version 10.3 (Régnière and St-Amant 2007, Régnière et al. 2014) and used to calculate mean monthly temperature, and total monthly precipitation. Mean-monthly maximum and minimum temperature, and total-monthly precipitation were used to calculate the monthly Climate Moisture Index (CMI) for each climate station (Figure 2.3). Climate Moisture Index is equal to precipitation minus potential evapotranspiration (derived from mean maximum and minimum temperatures) (Hogg 1997). BioSIM replaced any gaps in observed daily weather values at each climate station with observed daily weather from the eight closest climate stations weighted according to distance and elevation differences, or climate normals from the period 1921-1950, which were drawn from each climate station (Régnière et al. 2014). The 1921-1950 period was selected as it fell outside of the analysis window (1954-2014) and thus did not bias

interpolated data towards the early or late portions of either analysis period. Climate normals were only used when data were also missing from the eight stations used to interpolate missing data. This process was necessary to ensure that the daily climate record for each station was complete in order to run a climate correlation analysis.

2.2 Study Species

2.2.1 Jack pine

Jack pine is a dominant and commercially important conifer species in the Canadian boreal forest, and has the broadest distribution of any pine species in Canada (Figure 2.4) (Little 1971, Farrar 1995). Jack pine is a shade intolerant, pioneer species that typically appears after fire, where exposed mineral soil and abundant light provide ideal conditions for establishment (Rudolf and Laidly 2004). It is known for its ability to grow in lesser quality sites, such as on sand or gravel where other species are unable to survive, due to its long taproots that can reach depths of over two metres (Rudolf and Laidly 2004). In ideal growing conditions, jack pine trees can reach a height of up to 24 metres, but typically will reach 12 to 18 metres (Hosie 1990). In closed forest stands, jack pine stems grow thin and straight with little tapering of the main stem (Farrar 1995), which makes it valuable to industry for uses in poles, railway ties, and construction (Hosie 1990). Despite its ability to grow in drought prone environments, jack pine distribution has been shown to be moisture limited at its southern range limits (Hogg 1994, 1997, Brooks et al. 1998).

2.2.2 Lodgepole pine dwarf mistletoe

Dwarf mistletoes are obligate parasitic plants that infect species of conifers throughout the northern hemisphere (Richardson 1998). Lodgepole pine dwarf mistletoe, sometimes referred to as American dwarf mistletoe, is widely distributed in Canada, and can be found in British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario, as it coincides with the distribution of its host species (jack pine and lodgepole pine) (Figure 2.4) (Hawksworth et al. 2002, Natural Resources Canada 2014). This parasitic plant survives by appropriating water and nutrients from its host, which causes abnormal growth, decline in tree health, and mortality (Saskatchewan Ministry of Environment 2010), as well as reductions in wood quality (Piirto et al. 1974) and seed productivity (Moody and Amirault 1992). Extensive branching occurs at infected sites on

the tree, causing the characteristic dense branch clusters referred to as "witches' brooms" that make infection easily identifiable (McIntosh 2004). The formation of witches' brooms occurs three to five years after initial infection (Saskatchewan Ministry of Environment 2010). Dwarf mistletoe infection develops and spreads slowly, with a life cycle of five to six years from dispersal to reproduction (Hawksworth and Wiens 1996). In a newly infected stand there may be no obvious signs of infection until it has already spread. However, the vast majority of mistletoe seeds do not spread more than two to three metres from the source, and often just spread within the infected tree itself (Hawksworth 1965).

2.3 Study Design

2.3.1 Site Types

Three site types were established in each study region and classified on the basis of infection severity: healthy, infected, and mixed. Healthy sites were selected in jack pine stands where the majority of trees (>80%) were not infected. Infected sites were selected where the stand was composed of mostly infected trees (>80%). Mixed sites were stands composed of approximately half infected and half uninfected trees. Infection was determined by the presence of witches' brooms.

2.3.2 Field Data Collection

Environmental and site level data

At each site a 10 m by 10 m plot was set up, with the four corners marking each of the four cardinal directions. At the centre of the plot, coordinates were recorded using a Garmin E-trex Legend GPS unit. Elevation was also determined from the GPS. Aspect was determined using a compass and the direction of the plot corners. Percent slope was determined with a Suunto PM-5/ 360PC Clinometer. The landscape position of each site was recorded as crest, upper slope, lower slope, toe, or level (Table 2.2) (McLaughlan et al. 2010).

Vegetation and ground cover

Ground vegetation was assessed by an estimate of the percent cover of seven vegetation functional groups: lichen, moss, graminoids, deciduous shrubs, evergreen shrubs, forbs, and non-

flowering plants (horsetails, lycopods). The percent cover for other ground cover types was also estimated where applicable (litter, downed wood, rock, bare organic soil, and mineral soil).

Saskatchewan Forest Ecosite Designation

Ecosite designation was assigned using the Saskatchewan Forest Ecosite Designation System (McLaughlan et al. 2010). Each site was classified on the basis of canopy composition and dominant ground cover vegetation present. All sites keyed out as either BP2 or BP3 (Table 2.2, Figure 2.5). The BP2 ecosite (jack pine/lichen: moderately fresh sand) is primarily characterized by a canopy of ≥ 90% jack pine, and ground cover of ≥ 25% reindeer lichens (*Cladina* spp.). Additionally, BP2 sites often have large amounts of needle litter, have low species richness, and usually return to their former state following a disturbance. BP3 ecosites (jack pine/ feathermoss: moderately fresh loamy sand) are designated based on a canopy of ≥ 90% jack pine, and ground cover of < 25% reindeer lichens. Feathermosses, such as Schreber's moss (*Pleurozium schreberi*), are the dominant ground cover vegetation in the BP3 ecosites, and green alder (*Alnus viridis*), which is capable of fixing nitrogen, is a common understory species in the BP3 ecosites. Disturbance may alter the designation of this ecosite to a BP4 or BP5 (McLaughlan et al. 2010).

Soil data and moisture regime

Soil was examined at the south corner of each plot where possible, and if not (i.e., if there was too much woody debris, or rock, etc.), at the north corner. A section of soil was removed with a shovel in order to reveal the upper 20 cm of the soil profile. From this section, the depth of the organic layer and the depth of the A-horizon were measured with a measuring tape. A Dutch auger was then used to core the soil down to 1 m. The soil was hand textured to determine the effective texture at a depth of 1 m. The presence of gleying or mottling within the 1 m column of soil was also noted, as well as the depth at which it occurred. The moisture regime (Table 2.2) for each site was determined using a combination of ecosite type, soil texture, and presence of gleying or mottling, using the guidelines from the Field Guide to the Ecosites of Saskatchewan's Provincial Forests (McLaughlan et al. 2010).

Tree data and stand characteristics

The height and diameter at breast height (1.3 m) (DBH) was measured for all cored trees and all trees inside the plots. All cored trees were jack pine as this is the host tree of DM in the BPE, although other species were sometimes present and were included in within-plot tree measurements. Tree height was measured using a Nikon Forestry Pro laser rangefinder, and DBH was measured in centimetres with a Lufkin W606PM Diameter Pocket Tape. DBH measurements were used to calculate stand basal area as a metric of competition in each site. The number of trees inside the 10 m by 10 m plot was counted. For each tree, the species, whether it was alive or dead, and whether it was infected or not, was also recorded. Only standing trees were included in these counts. In cases where trees were broken or leaning, the trees were measured but a note was made of the condition.

Tree selection

The trees to be cored were selected systematically (Figure 2.6). In healthy plots ten trees were selected, one closest to each of the four corners and one closest to the centre inside the plot, plus five that were located outside the plot but closest to the centre. In mixed and infected plots it was not always possible to select trees in this manner. In cases where there were not enough trees in the plot that met the criteria, the remaining trees were selected from outside the plot. Infected trees were selected based on the infection level, where the most severely infected trees were preferred. If there were not enough trees categorized as 'severe', then less infected trees were chosen but it was noted that they were only 'moderately' infected. The criterion for 'severe' infection was determined where approximately ¾ or more of the live crown was infected, and 'moderate' when only about half of the live crown was infected. Infection was determined by the presence of witches' brooms. This method of characterizing DM infection was adapted from the standard 6-class DM rating system (Hawksworth 1977). The 6-class rating system was not practical for this study region, as frequently the only living branches left on the jack pine were restricted to the top of trees and difficult to see from the ground. Since I was seeking only severely infected trees for sampling, it was not necessary to determine infection level using the 6-class system only for using as a standard for characterization.

Tree cores

The selected trees were cored at breast height using a 5.1 mm Haglof ® increment borer. Two cores were taken from each tree, at right angles to one another. This was done to determine if there was any abnormal growth in one axis, such as reaction wood or fire scars, that may have impacted the inter-correlation of the ring width series. A total of ten trees were cored at healthy (n = 3 sites, n = 10 trees/site, n = 20 cores/site), and infected sites (n = 3 sites, n = 10 trees/site, n = 20 cores/site), a total of 20 trees were cored at mixed sites (n = 3 sites, n = 20 trees/site, n = 40 cores/site). In the entire study there were nine healthy, nine infected, and nine mixed sites (n = 27 sites), a total of 360 trees, and 720 cores. Cores were removed from the tree and placed into plastic straws for transport to the lab.

2.4 Tree Ring Analysis

2.4.1 Processing and measuring

The cores were air dried and glued onto grooved mounting boards, with the grain perpendicular to the surface of the board in order to best display the tree rings (Stokes and Smiley 1968). They were then sanded evenly with progressively finer sand paper (80, 120, 220, 320, 400, and 600 grit) using a belt sander. This process revealed the rings so they were clear enough to see cell boundaries and measure ring distances under a microscope. I measured each of the 720 cores using a Velmex stage (VoorTech 2014) and used the program measure J2X (VoorTech 2014) to capture ring-width measurements to 0.001 of a millimetre. All cores were measured perpendicular to the rings' orientation, starting from the bark and ending at or near the pith. All samples were taken before the end of the growing season, and were measured from the last complete ring.

2.4.2 Crossdating and standardization

Cores from each site were visually and statistically crossdated to assign the correct year to each ring, using the software COFECHA to assess the amount of common signal from the individual trees (Holmes 1983, Grissino-Mayer 2001). COFECHA flagged possible problems in cores where either the critical correlation level was not met or where the highest correlation produced was not at the correct year. I corrected errors where possible until all crossdated series surpassed a critical correlation level $\alpha = 0.01$ ($r = 0.4226$), based on overlapping 30-year

segments lagged by 15 years. Crossdated series were then standardized to remove any age related growth trends from the data. Standardization was done primarily using a modified negative exponential curve in R (R Core Team 2014) using the function 'detrend' in the package dplR (Bunn 2008, R Core Team 2014). In rare cases, cores that did not fit the modified negative exponential curve were assessed and an alternative curve (straight line, mean, or spline) was chosen on an individual basis, to ensure the growth pattern was estimated appropriately.

2.4.3 Chronology development

I created master chronologies in R using the function 'chron' in the dplR package (Bunn 2008, R Core Team 2014), which averaged the standardized time series to produce a unitless index of ring-width variation through time. Two types of master chronologies were produced: the standard chronology, and the residual chronology. The standard chronology was calculated by averaging all cores using a robust mean, while the residual chronology was additionally detrended with an autoregressive model to remove the autocorrelation and then averaged (Cook 1985, Bunn 2008). Master chronologies were developed in this manner for four groups (Healthy, Infected, Mixed-healthy, and Mixed-infected) for each study region (Northern, BERMS, Southern), by grouping individual site chronologies from Healthy sites, Infected sites, healthy trees from Mixed sites, and infected trees from Mixed sites. Grouping all trees together from Healthy only sites and Infected only sites simplified the analysis and facilitated comparison of chronologies of healthy trees from pure stands to infected trees from pure stands. Mixed sites presented an easy comparison of healthy and infected trees growing at the same site, while pure stands have no connection to one another and could not be compared in the same site-level, pairwise manner.

2.5 Statistical Analysis

2.5.1 Chronology descriptive statistics

Sample depth

Sample depth is the number of cores that contribute to a master chronology at a given point in time (Fritts 1976, Speer 2010). The greater the sample depth, the more reliable the chronology as a larger number of cores are used to create that chronology. Trees sampled for my analysis were not all of equal age. The result of sampling trees of different ages is that the sample

depth decreases the further back in time the chronology goes. Therefore, fewer cores were used to create each chronology at earlier points in time. The reliability of the chronology therefore degrades as the sample depth decreases, and the point at which this occurs varies between the different chronologies.

Series inter-correlation

The series inter-correlation is the average of all the correlations of individual cores against a master chronology made up of all cores in a group (Grissino-Mayer 2001). The correlation coefficient (*r*) is an important statistic in dendrochronology. It can range from -1.0 to 1.0, where -1.0 indicates a perfect negative correlation, 1.0 indicates a perfect positive correlation, and zero indicates no relationship between series. Pearson product moment correlation was used for this analysis, at a critical level of α=0.01 (r=0.4226) based on a segment length of 30 years. Series with an inter-correlation surpassing this critical value have a strong common signal, or relationship, between individual cores in a series (Grissino-Mayer 2001).

Expressed Population Signal

The Expressed Population Signal (EPS) is another measure of the strength of a common signal that is dependent on sample size and shared covariance among trees (Speer 2010). The common signal in a group of trees is the degree of similarity in how the ring widths vary through time in response to the environment. For a given degree of similarity, a greater sample size leads to a greater signal-to-noise ratio in a ring-width series. Fewer cores contributing to a chronology leads to more noise in the data, as individual tree variability is more prominent, and can mask a common signal. A chronology with an EPS value that exceeds 0.85 is considered suitable for climate analysis (Wigley et al. 1984, Speer 2010).

Mean Sensitivity

Mean sensitivity (MS) is the relative difference in ring width from one year to the next in a series. The values for MS can range from 0, when there is no difference in ring width from one year to the next, to 2, where a ring of zero width is succeeded by a ring with a non zero width (Fritts 1976). A complacent series will usually have a MS below 0.2, and a very sensitive series will have a value above 0.3 – 0.4 (Grissino-Mayer 2001, Speer 2010).

Autocorrelation

Autocorrelation is the influence of the previous-years' growth on the current-years' growth due to tree physiological processes. This can be described as a lag in the trees growth response to climate (Fritts 1976, Speer 2010). First-order autocorrelation (lag of 1 year) was removed during creation of the residual master chronologies with an autoregressive model (Cook 1985, Bunn 2008). The purpose of the residual chronology is to minimize noise in the time series, and maximize the signal of tree growth (Cook 1985).

2.5.2 Divergent chronologies

I did a piecewise regression analysis with a broken stick model (Toms and Lesperance 2003) to statistically assess the divergence point for each pair of healthy and infected chronologies within a geographic region. Broken stick models are useful for modeling thresholds, where two lines are joined at a breakpoint (Toms and Lesperance 2003). In this case, I modeled the point at which the growth pattern of infected trees changed from that of healthy trees. I first calculated the log (ratio) of the mean ring widths (Infected/ Healthy) at each point in time (Schwarz 2015). The mean-ring widths were calculated when creating the standard master chronology. A value of 0 for the log (ratio) indicated that the means of infected and healthy ring widths were not different (Schwarz 2015). I used a broken stick model on the log (ratio) of the means to search for a breakpoint in time where the mean-ring widths diverge (Schwarz 2015). To do this I used the function 'piecewise.linear' in the SiZeR package in R (Toms and Lesperance 2003, R Core Team 2014). Confidence intervals were calculated by bootstrapping 1000 samples, and significance was chosen to be $\alpha = 0.05$. I used this statistical approach to validate or discard my subjective choice of divergence year from my visual inspection of ring-width series.

2.5.3 Climate correlation analysis

I broke the master chronologies into two different 30-year segments: 1954-1983, and 1984-2014 to determine the relationship between radial growth (ring width) and climate over different time periods. The 1954-1983 segment served as a baseline for the past climate sensitivity in jack pine. For my purposes, climate sensitivity was defined as the months and direction (positive or negative) of the correlation coefficients. Changes in climate sensitivity were therefore changes in the correlated months, or changes in the direction of the correlation, that

were significant at $\alpha = 0.05$. The 1984-2014 segment was used to determine whether DM infection altered the climate sensitivity in infected versus healthy trees, using a recent climate window because the DM infection has only been present in the trees for a short period of time. The two 30-year windows were chosen to capture as much historical climate variability as possible, but a short enough time period to have two equal periods for comparison, and to capture any differences in climate sensitivity of the infected chronologies. I ran bootstrapped correlations between residual master chronologies and monthly climate variables (mean monthly temperature, total monthly precipitation, and monthly CMI) for the two different segments using the function 'dcc' in the bootRes package in R (Zang and Biondi 2012, R Core Team 2014). The 'dcc' function calculates bootstrapped correlations, emulating the functionality of the program DENDROCLIM2002 (Biondi and Waikul 2004). Coefficients are Pearson's correlation coefficients, and significance is tested at $\alpha = 0.05$.

I compared ring-width correlations with monthly climate variables between healthy and infected master chronologies within each site and between sites. I calculated correlations from April of the previous year, to September of the current year, to capture both the spring and summer of the previous and current year. For the next stage of my analysis, I used correlation with climate as a response variable to compare healthy and infected trees within and across the three study regions with a general linear model. I ran bootstrapped correlations between residual-master chronologies from individual sites and monthly climate variables (mean monthly temperature, total monthly precipitation, and monthly CMI) for the current spring and current summer months. I used the previous 30-years for these correlations (1984-2014) in an attempt to maximize the signal from infected trees, while capturing as much past climate variability as possible.

2.5.4 General linear models

I used the Pearson's correlation coefficients between ring widths and climate as response variables in a general linear model to assess drivers of climate sensitivity. Correlation coefficients were calculated between site residual master chronologies and climate variables (mean monthly temperature, total monthly precipitation, and monthly CMI), as described above. I grouped each of the three climate variables into two groups, current spring (representing the period of early season growth and respiration in April, May, June) and current summer (representing the period

of late season growth in July, August, September), for a total of six response variables to examine in six different general linear models. I used function 'glm' in R to fit a linear model, with a Gaussian error structure, and performed model selection for each response variable (Chambers and Hastie 1992, R Core Team 2014). First I fit a maximal model containing all explanatory variables that I hypothesized could explain variation in the response variable. The following explanatory variables were included in the maximal model: infection by study region interaction, site type, stands basal area, and tree height. Infection was included to determine whether DM was the main driver of differences in the climate response of trees. Study region was included to determine whether there was an effect of location in the regional moisture gradient, to address any potential effects of drought stress on the climate response of trees. The interaction term was used to address any effect of location in the regional moisture gradient on the response of healthy compared to infected trees. Site type was used as a potential explanatory variable to address any effect of pure versus mixed site type on the climate response of trees. Stand basal area and tree height were included to account for competition effects at each site.

I proceeded with model selection from the maximal model using the 'drop1' function from the Stats package to systematically assess the explanatory variables. The 'drop1' function selects which explanatory variables to remove from the model based on the effect on Akaike Information Criterion (AIC) values (Crawley 2007). AIC measures the fit between the model and the data, which balances explanatory power of model parameters with a penalty for the number of parameters (Crawley 2007). The goal is to achieve the simplest model with the most explanatory power (Crawley 2007). Lower AIC values indicate better fitting models (Sakamoto et al. 1986, Crawley 2007). This process was repeated until the removal of parameters from the model no longer improved the model in terms of AIC. From this point, second-order AIC (AICc) was used to rank potential models (Burnham et al. 2011). AICc is a bias correction for AIC when sample sizes are small (Burnham et al. 2011). The change in AICc (Δ AICc) was the main criterion for evaluating the best models. A value of < 2 for the Δ AICc was ideal, however, if the Δ AICc was < 2 for more than one model, then the simplest model was chosen (Burnham et al. 2011). When the Δ AICc was between 2 and 7 the AICc weight, log-likelihood, and evidence ratio were also used to evaluate models. Models with a Δ AICc in the range of 2 to 7 should not be discounted (Burnham et al. 2011). The R package AICcmodavg was used to calculate AICc, Δ AICc, AICc weight, log likelihood, and the evidence ratio (R Core Team 2014). The function 'summary' in

the base R package was used to assess the significance of model parameters and interactions (Chambers and Hastie 1992, R Core Team 2014).

Table 2.1: Coordinates and grouping of individual sites for each study region (Northern, BERMS, and Southern). Coordinates collected in UTM Zone 13, NAD 83 datum.

Study Region Name	Geographic Area	Type	Site ID	Group ID	Northing (m)	Easting (m)
Northern	Hwy 165 E/ Hwy 2	Healthy	NH1	NH	6067204	459217
		Healthy	NH2		6076002	480536
		Healthy	NH3		6061915	511332
		Infected	NI1	NI	6067715	458650
		Infected	NI2		6075990	480589
		Infected	NI3		6072595	481215
		Mixed	NM1	NM	6067234	458586
		Mixed	NM2		6074293	480333
		Mixed	NM3		6072671	481218
BERMS	Old Jack Pine	Healthy	BH1	BH	5973983	520672
		Healthy	BH4		5975992	524769
		Healthy	BH3		5973529	522095
		Infected	BI2	BI	5975870	525005
		Infected	BI4		5971896	523523
		Infected	BI3		5971899	523525
		Mixed	BM4	BM	5975823	524809
		Mixed	BM1		5973620	522166
		Mixed	BM5		5971870	523531
Southern	Fort à la Corne Island Forest			SH		
		Healthy	SH2		5903229	512881
		Healthy	SH3		5902822	508701
		Healthy	SH1		5903227	514515
		Infected	SI4	SI	5902859	511270
		Infected	SI3		5903225	512821
		Infected	SI2		5903172	513227
		Mixed	SM1	SM	5903213	513216
		Mixed	SM3		5902751	508720
		Mixed	SM2		5904114	509606

Table 2.2: Characteristics for 27 sites sampled between July and September 2015.

Site	Elev	Land	Slp	Asp	Ecor	Ecos	MR	Soil text	Date
NH1	509	U. Slope	-8%	S	Mid-Boreal	BP2	Mod. dry	Ls	Sept 3
NH2	356	U. Slope	-4%	E	Upland	BP3	Mod. dry	Sl	Sept 3
NH3	507	L. Slope	-2%	N		BP2	Very fresh	Ls	Sept 3
NI1	506	L. Slope	-7%	W		BP3	Mod. fresh	Ls	Sept 3
NI2	503	U. Slope	-3%	NW		BP2	Mod. dry	Sl	Sept 3
NI3	407	Toe	-4%	NE		BP3	Very fresh	Ls	Sept 3
BH1	517	L. Slope	-2%	SW		BP2	Fresh	S	June 9
BH4	509	U. Slope	-5%	NW		BP3	Very fresh	Ls	June 11
BH3	527	L. Slope	-4%	N		BP2	Fresh	Ls	June 12
BI2	523	Toe	-6%	E		BP3	Very fresh	Ls	June 11
BI4	506	U. Slope	0%	N/A		BP3	Very fresh	Ls	June 12
BI3	530	U. Slope	-2%	NW		BP3	Mod. dry	Ls	June 16
BM4	524	U. Slope	-6%	E		BP2	Mod. dry	Ls	June 11
BM1	504	Toe	-2%	SW		BP3	Mod. fresh	Ls	June 12
BM5	500	U. Slope	0%	N/A		BP3	Very fresh	Ls	June 12
SH2	458	L. Slope	-4%	W	Boreal	BP3	Very fresh	Ls	July 2
SH3	458	Level	-3%	E	Transition	BP3	Mod. dry	Ls	July 2
SH1	453	L. Slope	-30%	NW		BP3	Mod. dry	Ls	July 2
SI4	447	Level	-2%	NE		BP3	Very fresh	Sl	July 2
SI3	454	Level	-2%	N		BP3	Mod. dry	Ls	July 2
SI2	451	Level	-1%	SE		BP3	Mod. dry	Ls	July 2
SM1	457	L. Slope	-2%	N		BP3	Very fresh	Sl	July 2
SM3	460	L. Slope	-8%	W		BP3	Mod. dry	Ls	July 2
SM2	457	U. Slope	-5%	SE		BP2	Mod. dry	Sl	July 2

Notes: Elev – elevation (metres above sea level); Land – landscape position (U.Slope – Upper Slope, L. Slope – Lower Slope); Slp – slope; Asp – aspect; Ecor – Ecoregon; Ecos – ecosite; MR – moisture regime; Soil text – effective soil texture at 1 m depth (Ls – Loamy sand, Sl – Sandy loam, S -- Sand); Date – date sampled.

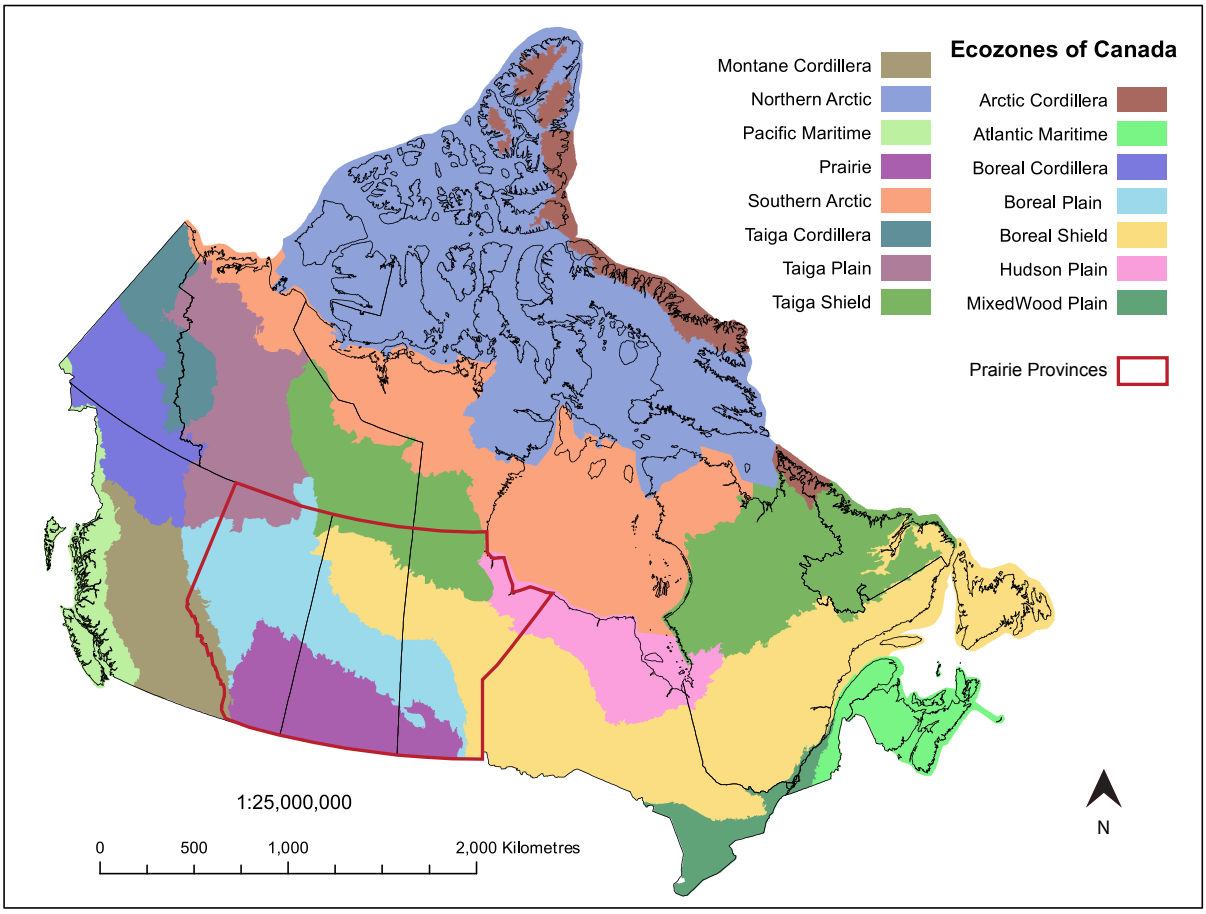

Figure 2.1: Map of the ecozones in Canada. Projected coordinate system: Canada Lambert Conformal Conic, NAD83. Source: Agriculture and Agri-Food Canada, ESRI.

Figure 2.2: Map of the Prairie Provinces (depicted by the red border) of Canada and the extent of the Boreal Plains Ecozone in Saskatchewan (green). Locations of study regions are also shown, illustrated by the red stars. Projected coordinate system: Web Mercator Auxillary Sphere, WGS84. Source: Agriculture and Agri-Food Canada, ESRI.

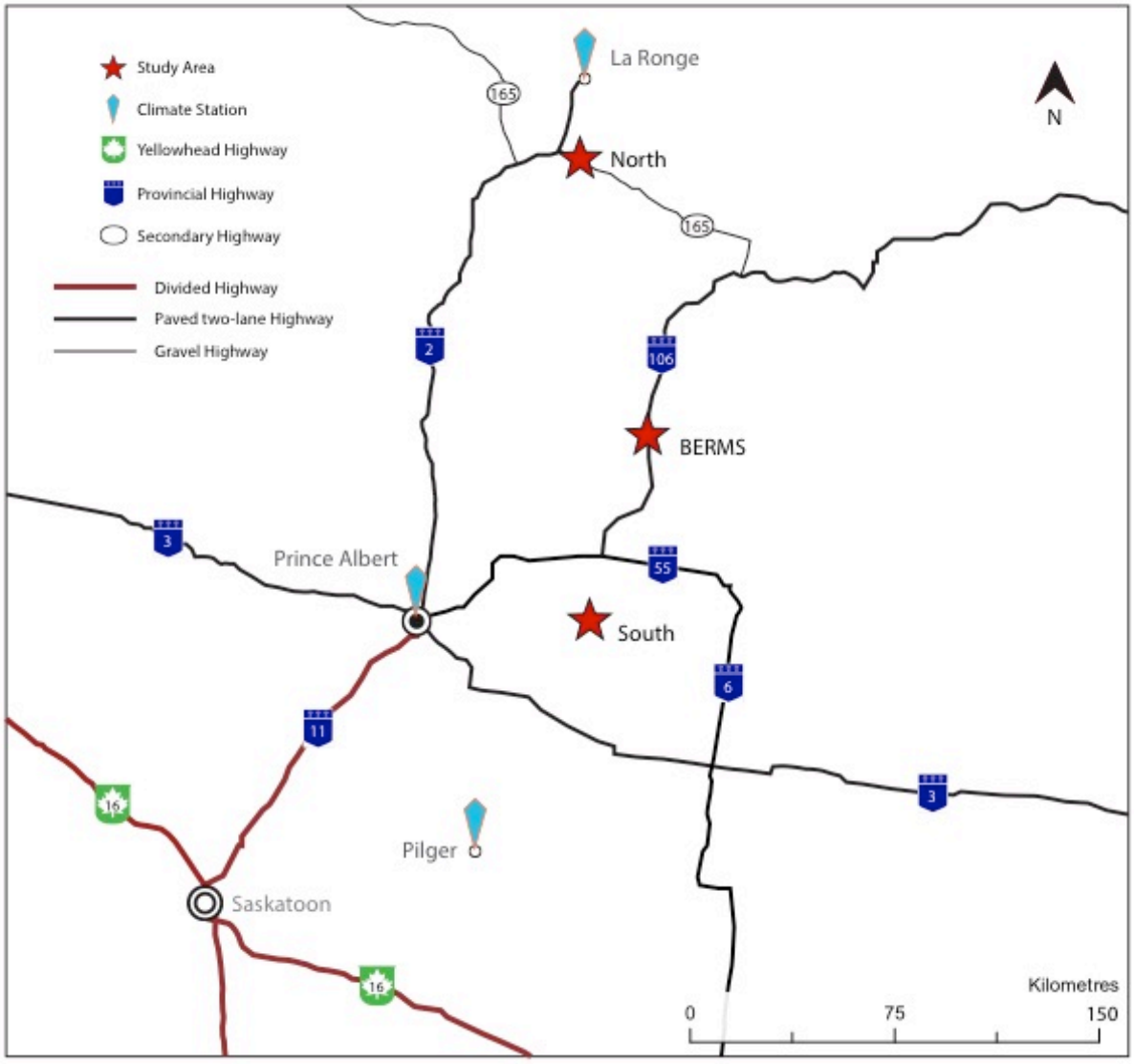

Figure 2.3: Locations of study regions in relation to climate stations used in central Saskatchewan. Projected coordinate system: Web Mercator Auxillary Sphere, WGS84. Source: ESRI.

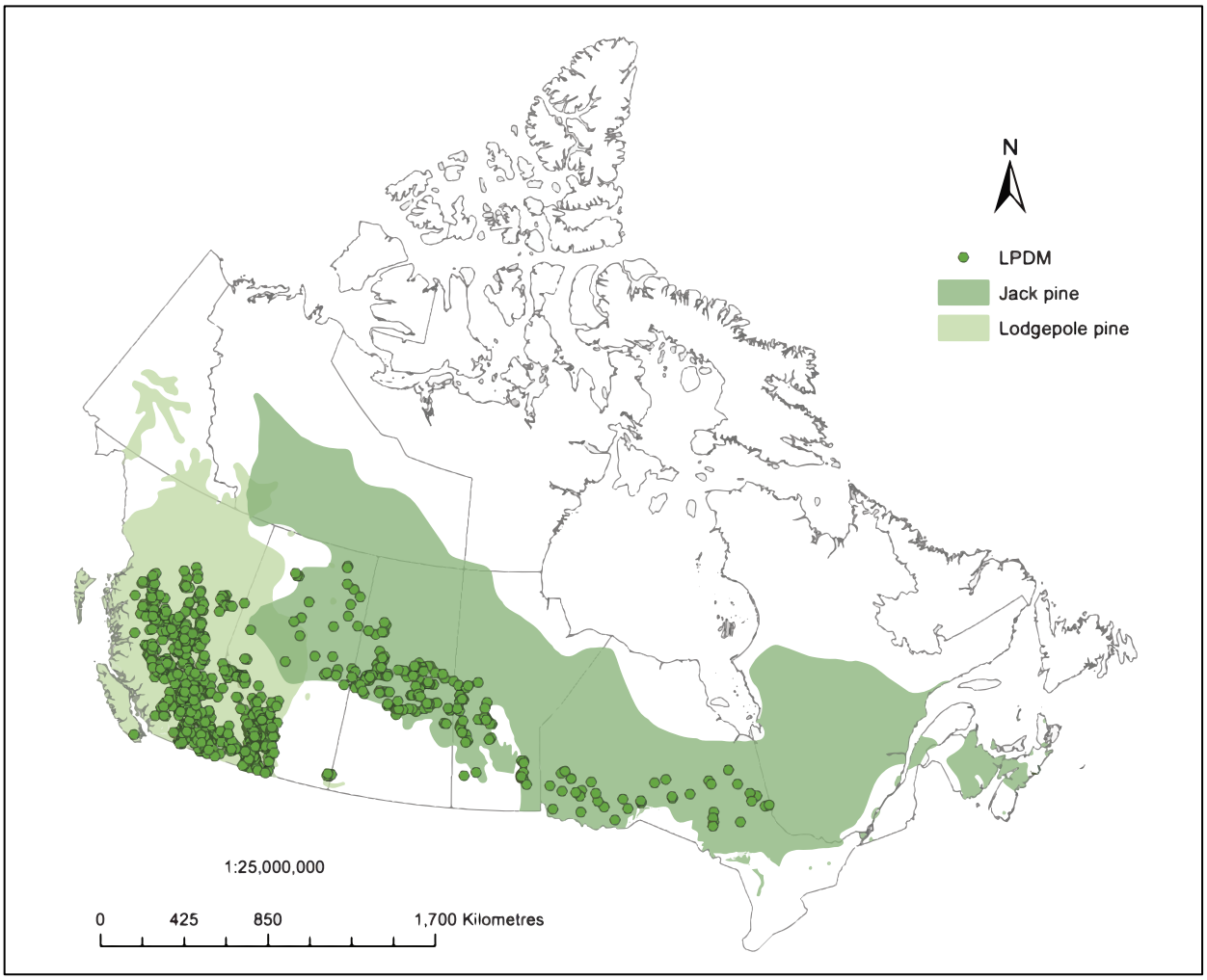

Figure 2.4: Distribution of lodgepole pine dwarf mistletoe (DM), jack pine and lodgepole pine in Canada. Projected coordinate system: Lambert Conformal Conic, NAD83. Source: ESRI, USGS, PSIS (NRCan).

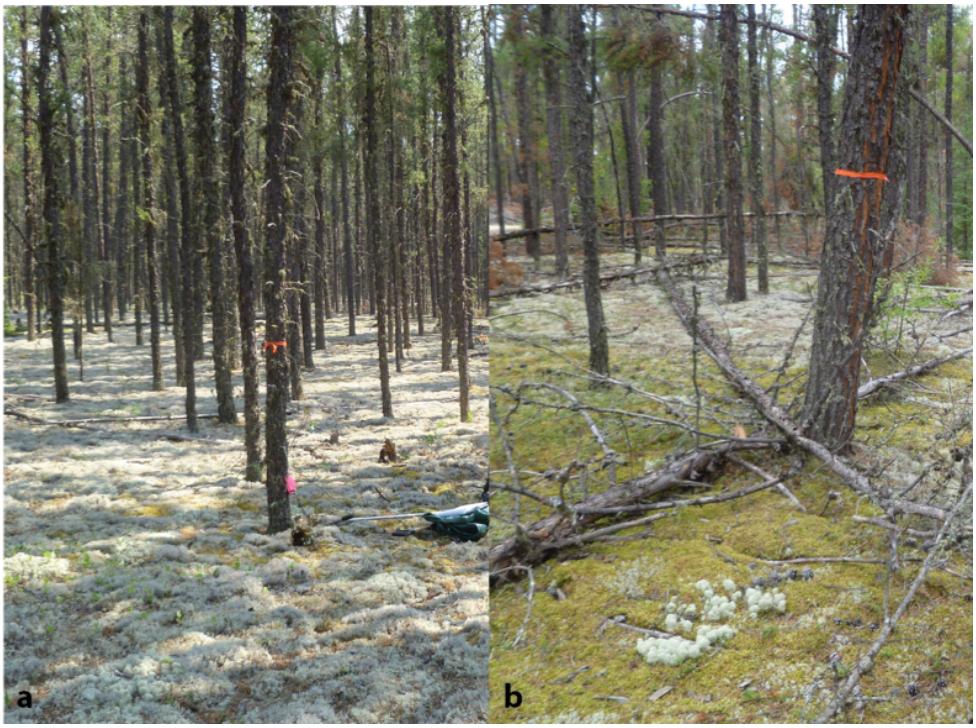

Figure 2.5: Saskatchewan ecosites BP2 (a) and BP3 (b).

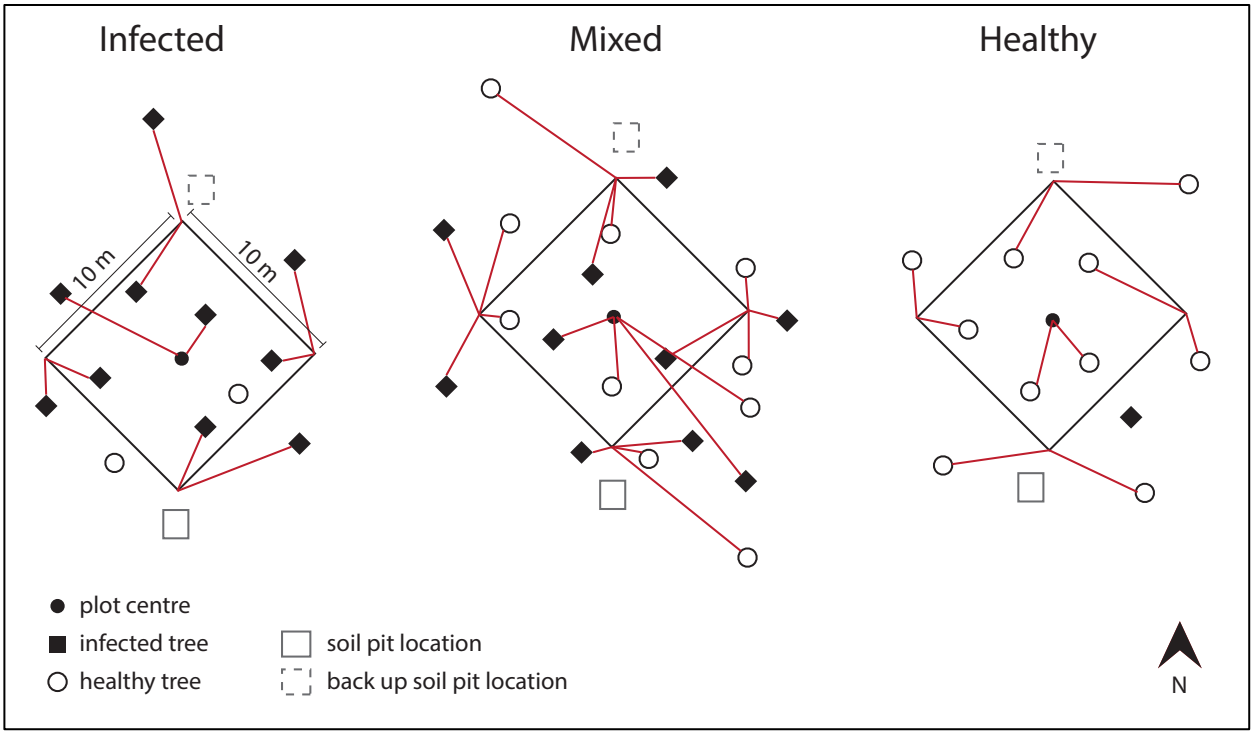

Figure 2.6: Diagram of plot set up and sampling design for each plot type (healthy, infected, and mixed). Red lines illustrate the trees selected in relation to the plot centre and corner points. Five trees closest to the plot centre and four corners inside and outside the plot were selected whenever possible (healthy trees in healthy sites, infected trees in infected sites). In mixed sites both healthy and infected trees were sampled in the same quantities.

CHAPTER 3

RESULTS

3.1 Description of Site Chronologies

Out of the 720 original cores collected across all study regions, 683 (94.9%) were retained in the three master chronologies (Table 3.1). Similarly, 355 of the 360 trees sampled (98.6%) remained in the final three chronologies. More cores and trees were retained in the final chronologies in the Northern and BERMS regions than in Southern region: 95.4% (229/240) of cores and 99.1% (119/120) of trees contributed to the master chronologies in the Northern and BERMS regions, while 93.7% (225/240) of cores and 97.5% (117/120) of trees were used in the final chronology in the Southern region. Cores were discarded from the final chronology only when they displayed a very weak or negative correlation with the rest of the chronology that could not be corrected. Sometimes this was due to the poor quality of the core, such as damage, which impaired accurate measurement, or abnormal growth that did not coincide with the majority of the cores in the chronology. In the Southern region, more cores were problematic for crossdating, particularly when infected, which is why a lower percentage of cores made it into the final chronologies.

3.1.1 Age, sample depth, and growth patterns

The average age of the trees from each of the three standard master chronologies was 126.7 years in the Northern region, 111.7 years at BERMS, and 92.7 years in the Southern region (Table 3.2). The variability in the age of the master chronologies decreased from the Northern region (s.d. = 29.8 years), to BERMS (s.d. = 10.1 years), to the Southern region (s.d. = 2.7 years). Due to this high variability in tree age between sites, the sample depth was not equal throughout the entire time span of each master chronology, particularly in the Northern and BERMS regions (Figures 3.1 and 3.2). Visual estimation of common years of above- and below-average radial growth for each study region was restricted to the time period where sample depth is greater than 30, or approximately half of the original sample depth. For the Northern region the common years of below-average radial growth in each master chronology were 1961, 1982, and 1995 (Figure 3.1). Above-average radial growth occurred in 1975 and 1984 in the Northern master chronologies. Below-average growth consistently occurred in 1964-1966, 1983, and 1995 in the

BERMS region, and 1955 and 1976 were years where above-average radial growth occurred in all BERMS chronologies (Figure 3.2). In the Southern region, radial growth was consistently below average in the years 1964, 1987, and 1995, and above average in 1976 and 1984 (Figure 3.3). Common patterns in radial growth become more difficult to visually detect after the mid-1990s (Figures 3.1-3.3).

3.1.2 Chronology statistics

All chronologies showed evidence of a common growth signal, based on a significant mean series inter-correlation value, $\alpha = 0.05$ ($r = 0.4226$) (Table 3.2). Additionally, all chronologies surpassed the EPS threshold (> 0.85), and values for MS ranged from 0.22 to 0.24 (Table 3.2), indicating reasonable sensitivity and sufficient sample size (from 1954 onward) for climate analysis (Table 3.3). Series inter-correlation values were the most variable in the Southern region sites, having both the highest and lowest values of individual sites in all regions. The lowest MS values occurred in the Northern region, and the highest occurred in the Southern region. Similarly, EPS values were the most consistent in the Northern region, and the most variable in the Southern region (Table 3.2).

3.2 Divergent Chronologies

3.2.1 Visual detection of divergence

Divergence between healthy and infected master chronologies was apparent in every study region, with few exceptions (Figures 3.4 to 3.6). The year of divergence varied from 1997 to 2008, and appeared to begin earlier in the two southernmost regions than in the Northern region. Divergence was determined when the plotted difference between the healthy and infected master chronologies (I – H) of each group changed from a positive or zero value to a negative value and remained negative. The only exceptions to this were the mixed sites BM4 (BERMS region) and SM3 (Southern region). A divergence year was not apparent at BM4, as there was no change in the difference between healthy and infected trees (BM4i-BM4h) at any point since 1980 (Figure 3.5c). At the mixed site SM3, divergence was indicated when the difference between healthy and infected trees became negative in 1997, however the difference between chronologies was not consistent after this point and eventually returned to zero (Figure 3.6d).

3.2.2 Change point detection with a broken stick model

Change points were detected prior to the visually chosen year in each study region, with only one exception (Table 3.4). For the NH/NI (Northern region, pure sites) chronologies, the change point detected by the model was the exact year that I had chosen visually. Most of the change point years found by the broken stick models were within five years prior to the year selected visually for a given pair of chronologies (H and I). In most cases, both time periods examined (common period for all trees in a chronology of 1920-2014 or 1930-2014 and 1950-2014) detected a similar change point within five years of the visually chosen point. In two cases, only one of the examined time periods was able to detect a change point within five years, and in another two cases neither time period was able to detect a similar change point. Interestingly, one of the latter sites was SM3, for which I was unable to visually select a reliable divergence point. However, the model selected a change point in one time period for BM4, for which I found no visual divergence point. Overall, the piecewise regression using the broken stick model consistently selected change points prior to the divergence years that I was able to visually detect. It was able to validate many of my choices of divergence within five years of my visual examination of the plotted master chronologies.

3.3 Climate Correlation Analysis

3.3.1 Temporal changes in regional climate

Climate in each study region changed from the early 30-year period to the more recent 30-year period (Figure 3.7). Temperatures increased in all regions, with the greatest increases occurring in the winter months. The greatest changes in climate occurred for June precipitation in all study areas. In the north, June precipitation decreased, while in the BERMS and Southern regions there was an increase. In the early 30-year period, the Northern region had higher total precipitation in June than the two southernmost regions, but this has reversed in the more recent 30-year period where the southernmost regions have 10-15 mm more total precipitation in June than the North.

Increases in precipitation also occurred in July, and decreases were observed in the winter months for the two southernmost regions. Small decreases in spring, summer, and winter precipitation occurred for the Northern region. Water deficits (CMI) decreased in the two southernmost regions from the early 30-year period to the recent 30-year period from March to

August. The greatest change occurred in June, where the deficit dropped from approximately -3 to near zero in the southernmost regions, but increased in the Northern region. In all study regions, the greatest moisture deficit occurred in August for both time periods, but has become less negative in the recent 30-years. Overall, the greatest moisture deficit occurs in the Southern region for both time periods, but the difference between the BERMS and Southern regions has become less pronounced in the recent 30-year period (Figure 3.7).

3.3.2 Temporal changes in climate sensitivity

Climate sensitivity changed through time across the three study regions, but differed between healthy and infected chronologies only in the most recent 30-year period examined. Comparisons were made between all chronologies in the previous 30-years to the healthy chronologies in the recent 30-years. Changes in climate sensitivity occurred in each region, most often with the correlation becoming stronger, but the direction remaining unchanged. The primary changes in the Northern region were towards a more prominent negative correlation with previous-September temperature and current-August moisture, and a less pronounced negative correlation with moisture in the previous winter months (Figure 3.8 and 3.9). Additionally, in the Northern region, there was a significant positive relationship with current-April temperature that was consistent through time. The Central region showed more change from the early 30-year period to the current 30-year period.

More prominent positive correlations with current-summer temperature occurred in the Central region. The negative correlation with current-August moisture became more pronounced in the recent 30-years. The correlation with previous-May moisture changed from positive to near zero or slightly negative, and the positive correlation with previous-June became stronger. Similarly, current-May and June correlations became less positive and more positive, respectively (Figure 3.10 and 3.11). Changes in the Southern region were reflective of the Central region. Correlations with previous-spring temperature became more prominent, and current spring more positive. Once again, the negative correlation with August moisture became more pronounced in this region as in the others. Positive correlations with previous-June and September, and current-June all became stronger in the recent 30-years (Figure 3.12 and 3.13). In general, there was an increase in the strength of correlations with climate variables across all regions. This increased sensitivity to climate may be indicative of a more stressful environment in the recent 30-years.

3.3.3 DM impact on climate sensitivity within study regions (1984-2014)

Northern region

The impact of DM infection on the climate sensitivity of jack pine in the Northern region was minimal. Only minor differences occurred in the correlation of healthy and infected residual master chronologies with the climate variables temperature, precipitation, and CMI (Figure 3.9). A change occurred in the correlation with current-August CMI in infected trees, where the correlation was significant in healthy trees and not significant in infected trees. However, the overall pattern in correlation values across the 18-month period (previous-April to current-September) did not vary considerably. Generally, positive correlations remained positive, and negative correlations remained negative from healthy to infected trees (Figure 3.9).

BERMS region

DM infection had a larger impact on the climate sensitivity of trees in the BERMS region than it did in the Northern region. In healthy trees there was a significant positive correlation between radial growth and previous and current-June moisture (precipitation and CMI), which is not present in infected trees (Figure 3.11). The correlation with previous and current-June moisture variables was close to zero in the infected trees. Additionally, the correlation with temperature changed from healthy to infected trees as well. There was a significant positive relationship between radial growth and current-August and September temperature in healthy trees that was not present in infected trees. In the infected trees, there was a significant positive correlation with current-March and April temperature that was not apparent in the healthy trees. The positive relationship with temperature shifted from late summer in healthy trees to early spring in infected trees (Figure 3.11).

Southern region

The effects of DM on climate sensitivity of infected trees in the Southern region were different from that in the Northern region, but similar in some cases to the BERMS region. Similar to BERMS, there was a change in the response of ring width to previous and current-June moisture (precipitation and CMI) (Figure 3.13). In the Southern region, healthy trees had a positive correlation between radial growth and previous and current-June moisture, but this relationship was near zero for previous-June and marginally negative for current-June in infected

trees. There was also a significant negative relationship with current-February moisture in infected trees that was near zero in healthy trees. This negative relationship was present in both healthy and infected trees in the BERMS region, though only significant in infected trees. The relationship with temperature also differed between healthy and infected trees. Healthy trees had a significant negative correlation with previous-May that did not occur in infected trees. Additionally, infected trees had significant positive correlations with previous and current-April that were absent from healthy trees. Overall, infected trees had more negative correlations with moisture, and more positive correlations with temperature compared to healthy trees (Figure 3.13).

3.4 DM Infection and Climate

I assessed various factors affecting the growth-climate relationship across the study region, which included infection by study region interaction, site type, stand basal area, and tree height. The general linear models with the most explanatory power most commonly included infection by study region interaction (Table 3.5). Correlations between ring width and summer temperature were different in healthy and infected trees in all study regions ($p < 0.001$) (Table 3.6). In the Northern region, no other climate variables showed any differences between healthy and infected trees. Correlations with summer temperature differed between healthy and infected trees in the BERMS and Southern regions. Healthy trees in the BERMS region were positively correlated to late summer temperature, but the correlation was reduced to half the healthy correlation value in the infected trees (Figure 3.14). Other individual parameters that were significant to the climate-radial growth relationship in some cases were study region and tree height. Study region was significant for two climate variables: summer temperature and summer CMI (Table 3.6). In both cases the Northern region was significantly different from the BERMS and Southern regions ($p < 0.001$). For summer temperature, the Northern region was negatively correlated, while the BERMS and Southern regions were both positively correlated with radial growth (Figure 3.14). For summer CMI, the Northern region was near a zero correlation, while the BERMS and Southern regions were more negatively correlated (Figure 3.14). Tree height was also a significant parameter for two climate variables: spring precipitation ($p = 0.021$), and spring CMI ($p = 0.043$).

3.5 DM Infection Across a Latitudinal Gradient

For all climate variables there was variability across the study regions between healthy and infected trees (Figure 3.14). The impact of DM across a latitudinal gradient was assessed by the interaction between infection and study region. There was a significant interaction between infection and the Southern study region for two climate variables: spring precipitation ($p = 0.079$) and spring CMI ($p = 0.034$). The interaction for the variables spring precipitation and spring CMI showed the same pattern. This pattern showed the correlation between ring width and the climate variables diverged from the Northern to the Southern region, where healthy trees show a positive correlation, and infected trees show a negative relationship with both climate variables (Figure 3.14).

Table 3.1: Number of trees and cores used in final chronologies.

Study region	Site type	Original trees	Original cores	Actual trees	Actual cores
Northern	Healthy	30	60	29	55
	Infected	30	60	30	58
	Mixed-healthy	30	60	30	58
	Mixed-infected	30	60	30	58
BERMS	Healthy	30	60	30	58
	Infected	30	60	29	56
	Mixed-healthy	30	60	30	58
	Mixed-infected	30	60	30	57
Southern	Healthy	30	60	30	60
	Infected	30	60	29	54
	Mixed-healthy	30	60	30	59
	Mixed-infected	30	60	28	52

Note: Original trees – the total number of trees sampled; Original cores – the total number of cores; Actual tree – the number of trees used in final chronologies; Actual cores – the number of cores used in final chronologies.

Table 3.2: Statistics of the final standard chronologies.

Study region	Site type	R	EPS	MS	AR	Age
Northern	H	0.546	0.934	0.228	0.854	82
	I	0.595	0.934	0.225	0.861	141
	Mh	0.561	0.932	0.210	0.883	143
	Mi	0.551	0.939	0.214	0.887	141
BERMS	H	0.580	0.951	0.220	0.898	97
	I	0.501	0.915	0.243	0.856	120
	Mh	0.517	0.93	0.242	0.887	114
	Mi	0.540	0.929	0.249	0.879	116
Southern	H	0.646	0.95	0.256	0.842	96
	I	0.540	0.933	0.248	0.822	91
	Mh	0.514	0.938	0.227	0.852	90
	Mi	0.475	0.906	0.238	0.873	94

Note: Site type (H: Healthy; I: Infected; Mh: Mixed-healthy; Mi: Mixed-infected); R – Series inter-correlation; EPS –Expressed Population Signal averaged across entire chronology; Mean – Mean ring width (mm); SD – Standard deviation of ring width; MS – Mean Sensitivity; AR – 1st order Autocorrelation; Age – age of master chronology in years.

Table 3.3: Summary of 10-year segment in each chronology where EPS value falls below the 0.85 cut-off value.

Study region	Site Type	Start year	Mid year	End year	Sample depth	EPS
Northern	H	1941	1945	1950	42	0.822
	I	1931	1935	1940	34	0.771
	Mh	1901	1905	1910	30	0.814
	Mi	1901	1905	1910	34	0.77
BERMS	H	NA	NA	NA	NA	NA
	I	1910	1914	1919	29	0.813
	Mh	1945	1949	1954	56	0.787
	Mi	1945	1949	1954	52	0.748
Southern	H	1945	1949	1954	46	0.798
	I	1950	1954	1959	53	0.803
	Mh	1950	1954	1959	57	0.616
	Mi	1955	1959	1964	55	0.71

Note: Site type (H: Healthy; I: Infected; Mh: Mixed-healthy; Mi: Mixed-infected); Start year – the first year of the 10-year window examined; Mid year – the middle year of the 10-year window examined; End year – the last year of the 10-year window examined; Sample depth – the number of cores remaining in the 10 year window; EPS – Expressed Population Signal over the 10-year window examined.

Table 3.4: Summary of results from piecewise linear regression to estimate divergence between infected and healthy chronologies by study region and time period examined.

Study region	Chronologies	Time period	Threshold alpha	CI - lower	CI - upper
Northern	NH/NI	1930-2014	**2008**	**1975**	**2009**
		1950-2014	1976	1973	2009
	NM1h/NM1i	1930-2014	1999	**1997**	**2004**
		1950-2014	1999	**1996**	**2002**
	NM2h/NM2i	1930-2014	2003	**2001**	**2006**
		1950-2014	2004	**2001**	**2007**
	NM3h/NM3i	1930-2014	1999	**1992**	**2008**
		1950-2014	1995	**1985**	**2003**
BERMS	BH/BI	1920-2014	1993	1986	1995
		1950-2014	1985	1980	1991
	BM1h/BM1i	1920-2014	2000	**1956**	**2004**
		1950-2014	1999	**1998**	**2001**
	BM4h/BM4i*	1920-2014	1956	1936	1979
		1950-2014	2003	**1961**	**2007**
	BM5h/BM5i	1920-2014	1956	1936	2007
		1950-2014	2005	1962	2007
Southern	SH/SI	1920-2014	2001	**1987**	**2002**
		1950-2014	2001	**1987**	**2002**
	SM1h/SM1i	1920-2014	2000	**1998**	**2001**
		1950-2014	2000	**1999**	**2001**
	SM2h/SM2i	1920-2014	1958	1949	2001
		1950-2014	2001	1969	2003
	SM3h/SM3i	1920-2014	1983	1956	1988
		1950-2014	1967	**1965**	**2007**

Notes: Threshold alpha = the year at which the regression line changes slope, or the 'change point'; CI = Confidence interval, with lower and upper bounds ($\alpha = 0.05$) Grey shading indicates the date selected by the model was within 5 years prior to the date selected visually. Bolded confidence bounds indicate that the year selected visually was within the models' confidence interval. Grey shaded and bolded indicates the year selected by the model was the exact year selected visually. * indicates year was undetectable visually.

Table 3.5: Summary of general linear model selection for each climate variable using AICc. Maximal model = infection*study region + site type + stand basal area + tree height, Null model = 1.

Model Name	ΔAICc	AICc weight	Log likelihood	Evidence ratio	Goodness of Fit
Spring Temperature					
NULL	**0**	**0.54**	**21.77**	**NA**	**0.00**
infection*study region + height	**0.47**	**0.43**	**30.02**	**1.26**	**0.37**
infection*study region + site type + height	5.61	0.03	31.18	16.54	0.41
Maximal	9.6	0	31.29	121.69	0.41
Summer Temperature					
infection*study region + height	**0**	**0.98**	**39.55**	**NA**	**0.70**
Maximal	8.04	0.02	41.37	55.72	0.73
NULL	26.91	0	17.61	698422.9	0.00
Spring Precipitation					
infection*study region + stand basal area + height	**0**	**0.72**	**30.03**	**NA**	**0.47**
NULL	2.1	0.25	18.7	2.86	0.00
Maximal	6.96	0.02	30.59	32.52	0.48
Summer Precipitation					
NULL	**0**	**0.96**	**43.43**	**NA**	**0.00**
infection*study region + stand basal area	6.38	0.04	48.73	24.28	0.25
Maximal	14.09	0	50.71	1148.13	0.33
Spring CMI					
infection*study region + stand basal area + height	**0**	**0.79**	**26.58**	**NA**	**0.48**
NULL	2.94	0.18	14.83	4.36	0.00
Maximal	6.43	0.03	27.41	24.86	0.50
Summer CMI					
infection + study region	**0**	**0.94**	**50.78**	**NA**	**0.39**
infection + study region + stand basal area	5.91	0.05	50.82	19.2	0.39
NULL	10.05	0.01	41.93	152.36	0.00
Maximal	19.56	0	51.49	17720.54	0.412

Notes: ΔAICc – change in AICc, the best model has a value of zero; AICc weight – support for each model relative to other models, the best model has highest weight; Evidence ratio – comparison of best model against other models, Goodness of Fit – 1- (Residual Deviance / Null Deviance).

Table 3.6: Summary of parameters included in the best model for each response variable.

Model parameters	Estimate	SE	t value	Pr(>|t|)
Spring Temperature				
(Intercept)	0.062	0.0223	2.759	0.009**
Summer Temperature				
(Intercept)	0.12	0.119	1.014	0.319
Infection	-0.195	0.052	-3.756	< 0.001***
Northern region	-0.288	0.052	-5.548	< 0.001***
Southern region	-0.089	0.053	-1.684	0.103
Height	0.009	0.008	1.233	0.228
Infection x Northern region	0.106	0.074	1.428	0.164
Infection x Southern region	0.101	0.073	1.37	0.181
Spring Precipitation				
(Intercept)	-0.341	0.162	-2.1	0.045*
Infection	-0.026	0.071	-0.371	0.714
Northern region	0.079	0.069	1.143	0.263
Southern region	0.006	0.077	0.078	0.939
Stand Basal Area	0.0002	0.0003	0.722	0.476
Height	0.024	0.01	2.439	0.021*
Infection x Northern region	-0.113	0.102	-1.104	0.279
Infection x Southern region	-0.181	0.099	-1.825	0.079.
Summer Precipitation				
(Intercept)	-0.07	0.012	-5.69	< 0.001***
Spring CMI				
(Intercept)	-0.381	0.179	-2.131	0.042*
Infection	-0.024	0.078	-0.306	0.762
Northern region	0.11	0.076	1.446	0.159
Southern region	0.072	0.085	0.844	0.406
Stand Basal Area	0.0002	0.0003	0.658	0.516
Height	0.023	0.011	2.115	0.043*
Infection x Northern region	-0.138	0.113	-1.228	0.23
Infection x Southern region	-0.243	0.109	-2.228	0.034*
Summer CMI				
(Intercept)	-0.023	0.021	-1.123	0.27
Infection	0.018	0.021	0.881	0.385
BERMS region	-0.101	0.026	-3.96	< 0.001***
Southern region	-0.094	0.026	-3.68	< 0.001***

Notes: Significance codes: '.' p = 0.1; '*' p = 0.05; '**' p = 0.01; '***' p = 0.001.

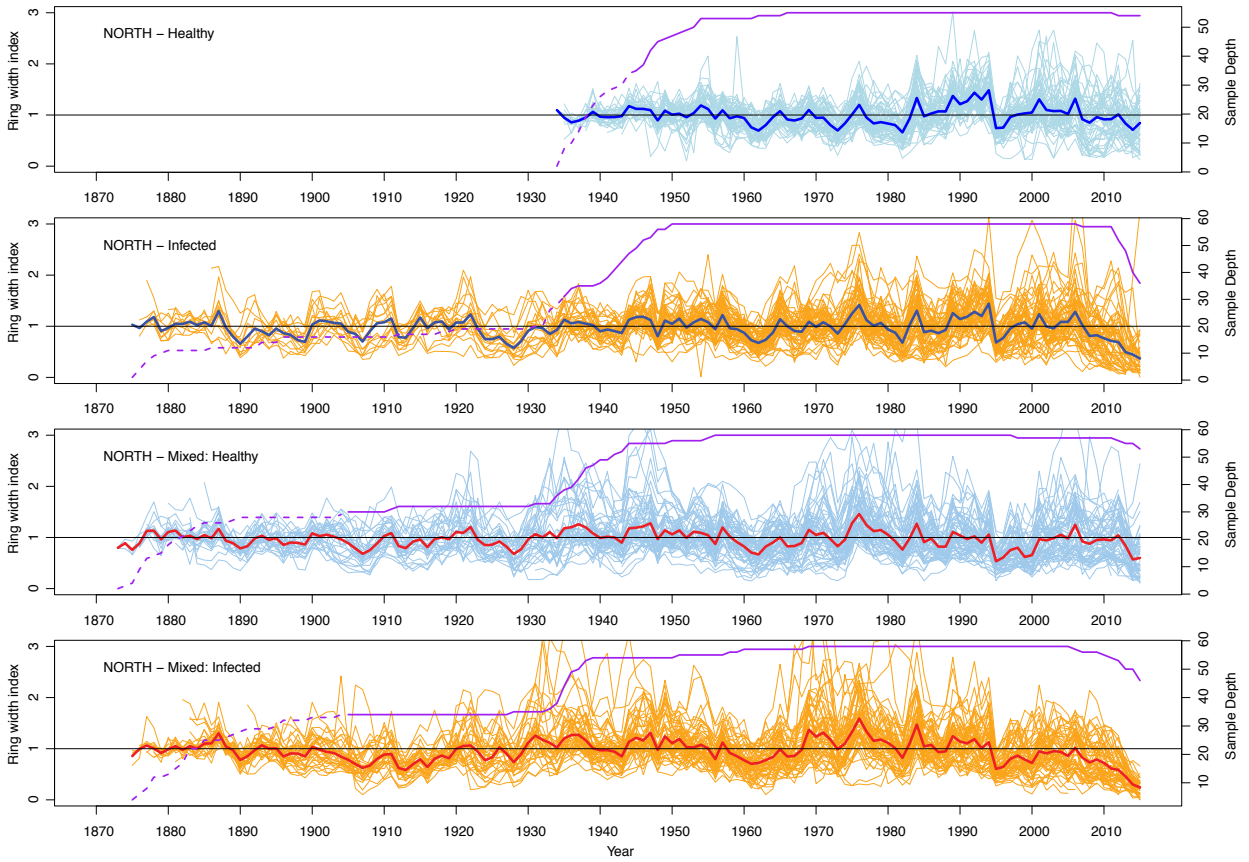

Figure 3.1: Northern region standard chronologies grouped by site type, where light blue represents healthy trees, and orange represents infected trees. The master chronology line is blue for pure sites (healthy only or infected only), and red for mixed sites. The left y-axis is a ring width index, the right y-axis is the sample depth (number of cores), and the x-axis is the time in years. The darker line represents the final master chronology, and the lighter lines represent the individual cores within each chronology. Above-average growth occurred in years when the master chronology is above the grey horizontal line, and below-average growth when it is below. The dashed/solid purple line is the sample depth of cores used in each year to create the master chronology. The purple line is solid where the EPS value is above 0.85, and dashed where the EPS is below 0.85.

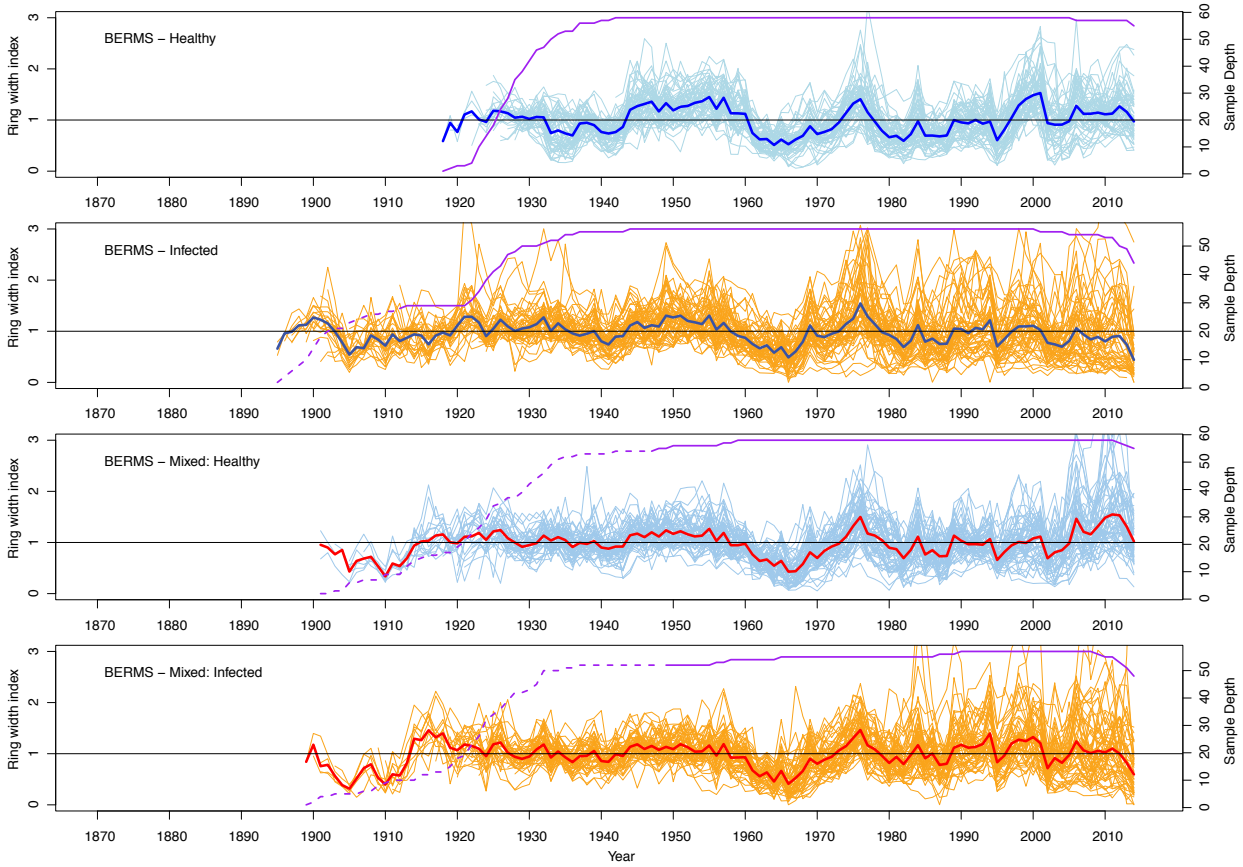

Figure 3.2: BERMS region standard chronologies grouped by site type, where light blue represents healthy trees, and orange represents infected trees. The master chronology line is blue for pure sites (healthy only or infected only), and red for mixed sites. The left y-axis is a ring width index, the right y-axis is the sample depth (number of cores), and the x-axis is the time in years. The darker line represents the final master chronology, and the lighter lines represent the individual cores within each chronology. Above-average growth occurred in years when the master chronology is above the grey horizontal line, and below-average growth when it is below. The dashed/solid purple line is the sample depth of cores used in each year to create the master chronology. The purple line is solid where the EPS value is above 0.85, and dashed where the EPS is below 0.85.

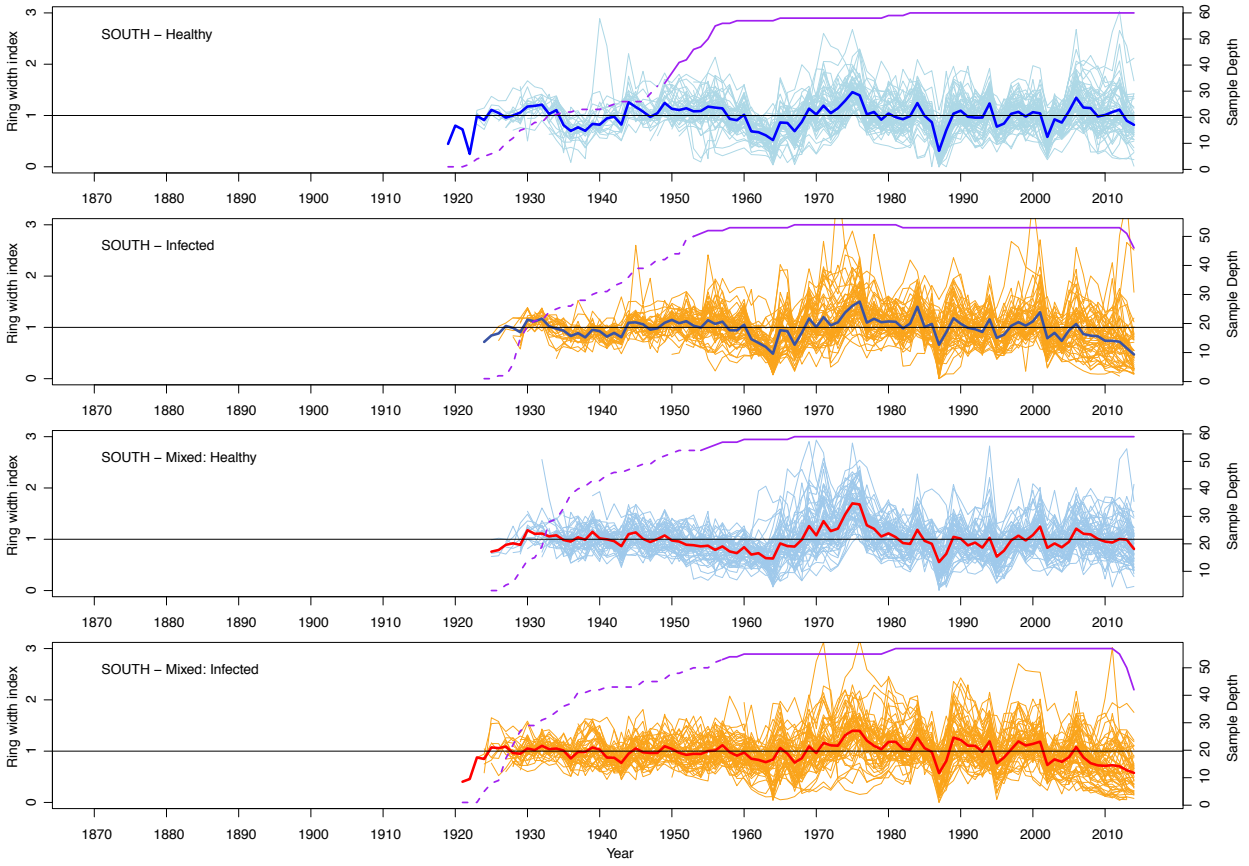

Figure 3.3: Southern region standard chronologies grouped by site type, where light blue represents healthy trees, and orange represents infected trees. The master chronology line is blue for pure sites (healthy only or infected only), and red for mixed sites. The left y-axis is a ring width index, the right y-axis is the sample depth (number of cores), and the x-axis is the time in years. The darker line represents the final master chronology, and the lighter lines represent the individual cores within each chronology. Above-average growth occurred in years when the master chronology is above the grey horizontal line, and below-average growth when it is below. The dashed/solid purple line is the sample depth of cores used in each year to create the master chronology. The purple line is solid where the EPS value is above 0.85, and dashed where the EPS is below 0.85.

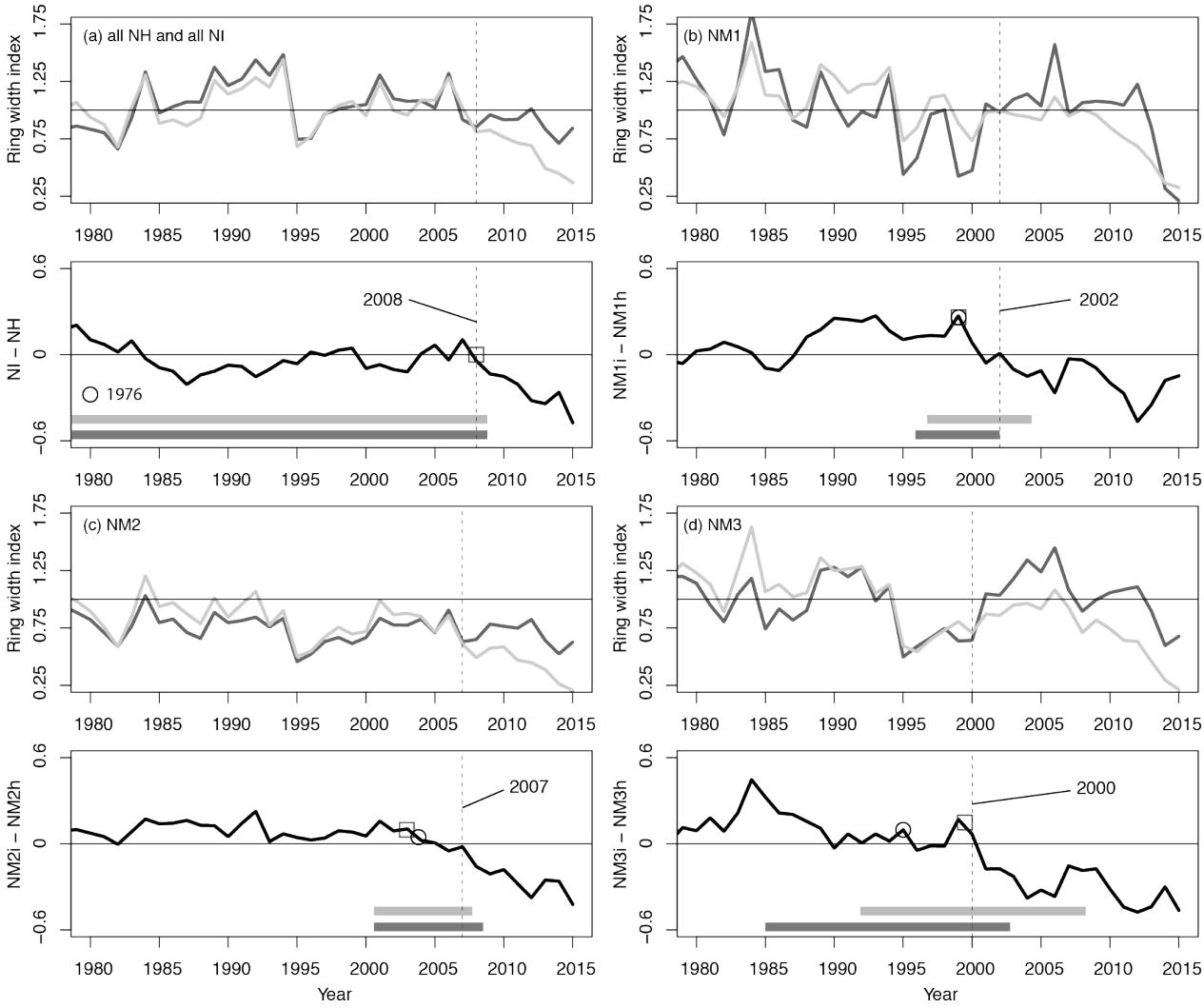

Figure 3.4: Healthy (dark grey) and Infected (light grey) standard master chronologies for (a) Healthy and Infected sites and (b-d) Mixed sites in the Northern region. The black lines represent the Infected minus the Healthy chronology for each group (a) NI-NH; (b) NM1i-NM1h; (c) NM2i-NM2h; and (d) NM3i-NM3h. The vertical dashed line indicates the year at which the healthy and infected chronologies visually diverge. The 1930-2014 period is represented by a square indicating the date selected by the broken stick model and the light grey horizontal line illustrates the confidence bounds ($\alpha = 0.05$) of the model. The circle and darker grey horizontal line represents the 1950-2014 model. Change point dates before 1980 are shown in the lower left corner. Lower confidence bounds prior to 1980 are not shown.

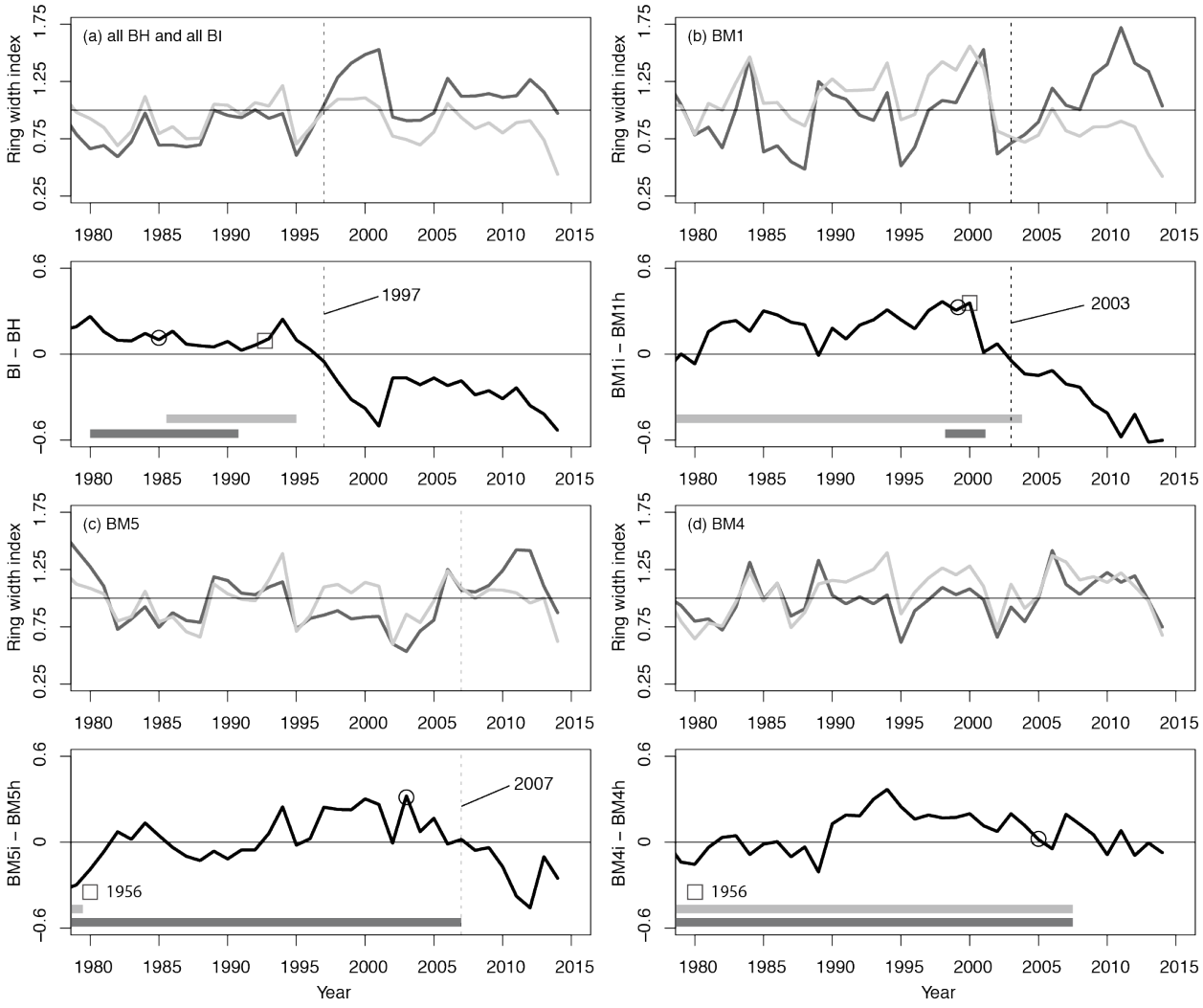

Figure 3.5: Healthy (dark grey) and Infected (light grey) standard master chronologies for (a) Healthy and Infected sites and (b-d) Mixed sites in the BERMS region. The black lines represent the Infected minus the Healthy chronology for each group (a) BI-BH; (b) BM1i-BM1h; (c) BM4i-BM4h; and (d) BM5i-BM5h. The vertical dashed line indicates the year at which the healthy and infected chronologies visually diverge. The 1920-2014 period is represented by a square indicating the date selected by the broken stick model and the light grey horizontal line illustrates the confidence bounds ($\alpha = 0.05$) of the model. The circle and darker grey horizontal line represents the 1950-2014 model. Change point dates before 1980 are shown in the lower left corner. Lower confidence bounds prior to 1980 are not shown.

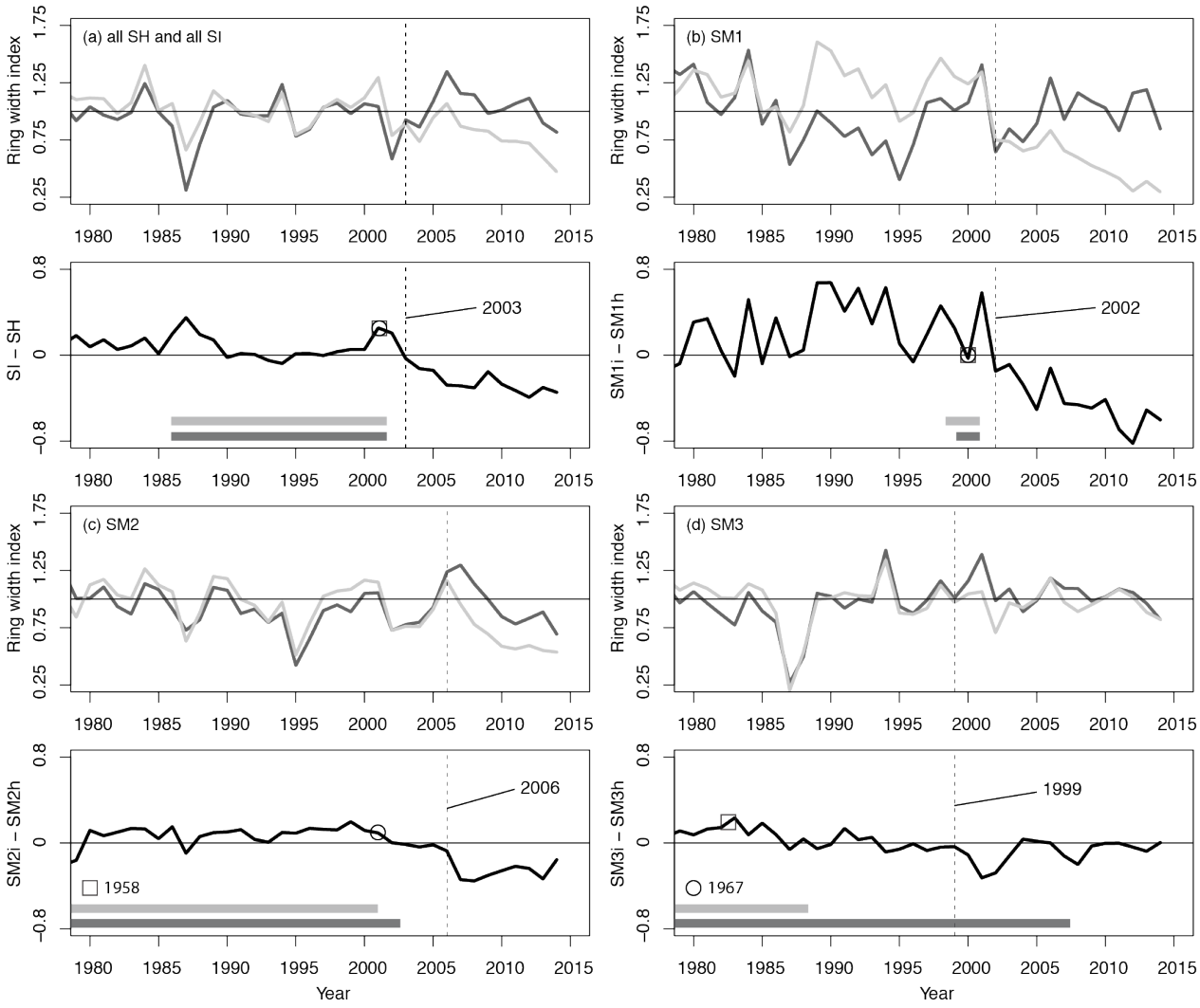

Figure 3.6: Healthy (dark grey) and Infected (light grey) standard master chronologies for (a) Healthy and Infected sites and (b-d) Mixed sites in the Southern region. The black lines represent the Infected minus the Healthy chronology for each group (a) SI-SH; (b) SM1i-SM1h; (c) SM2i-SM2h; and (d) SM3i-SM3h. The vertical dashed line indicates the year at which the healthy and infected chronologies visually diverge. The 1920-2014 period is represented by a square indicating the date selected by the broken stick model and the light grey horizontal line illustrates the confidence bounds ($\alpha = 0.05$) of the model. The circle and darker grey horizontal line represents the 1950-2014 model. Change point dates before 1980 are shown in the lower left corner. Lower confidence bounds prior to 1980 are not shown.

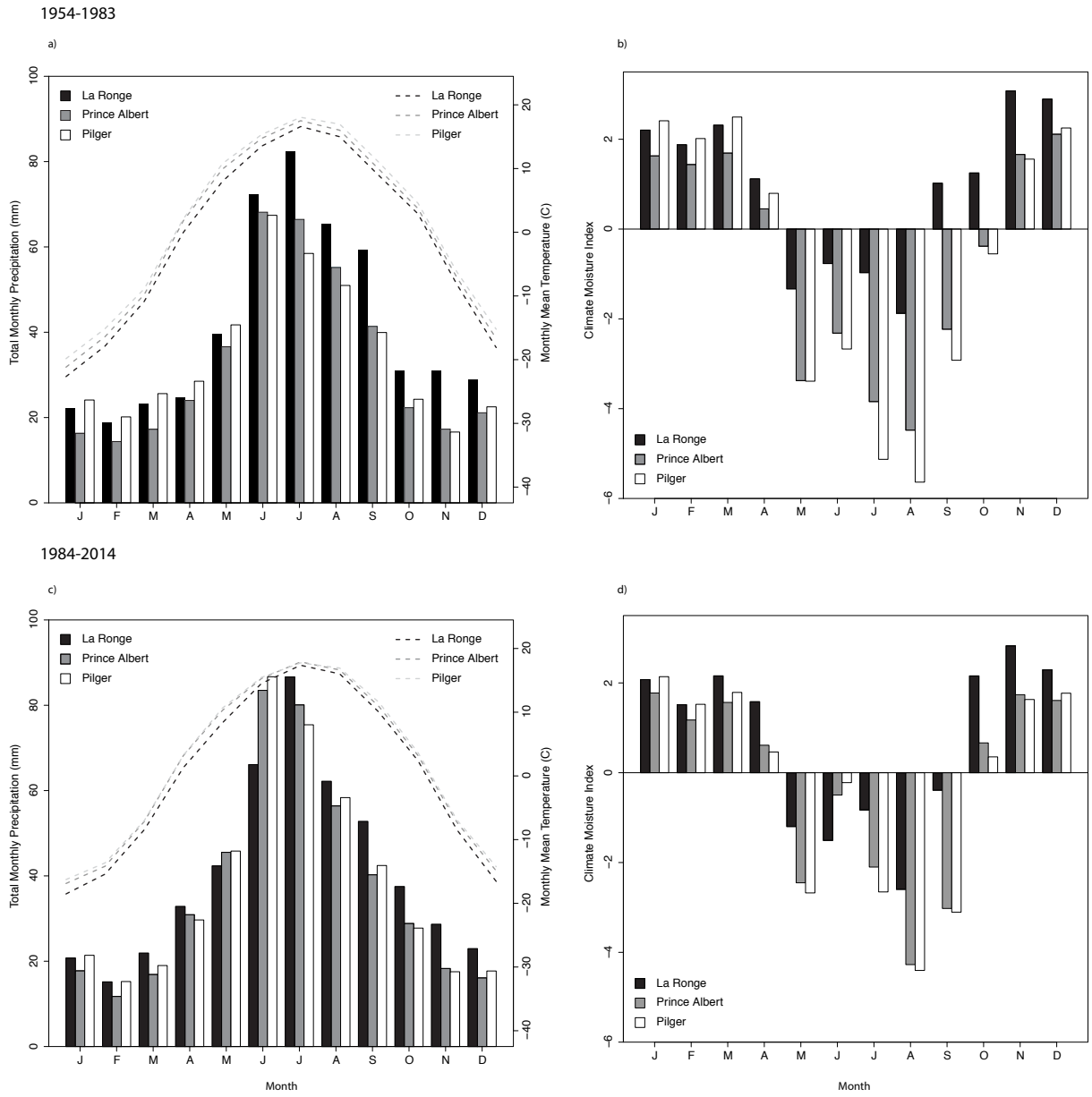

Figure 3.7: Average historical climate for the three climate stations for the time periods 1954 – 1983 (a and b), and 1984-2014 (c and d). Total monthly precipitation (mm) (left y-axis), mean monthly temperature (degrees C) (right y-axis), and Month (x-axis), and Climate moisture index (y-axis) and Month (x-axis).

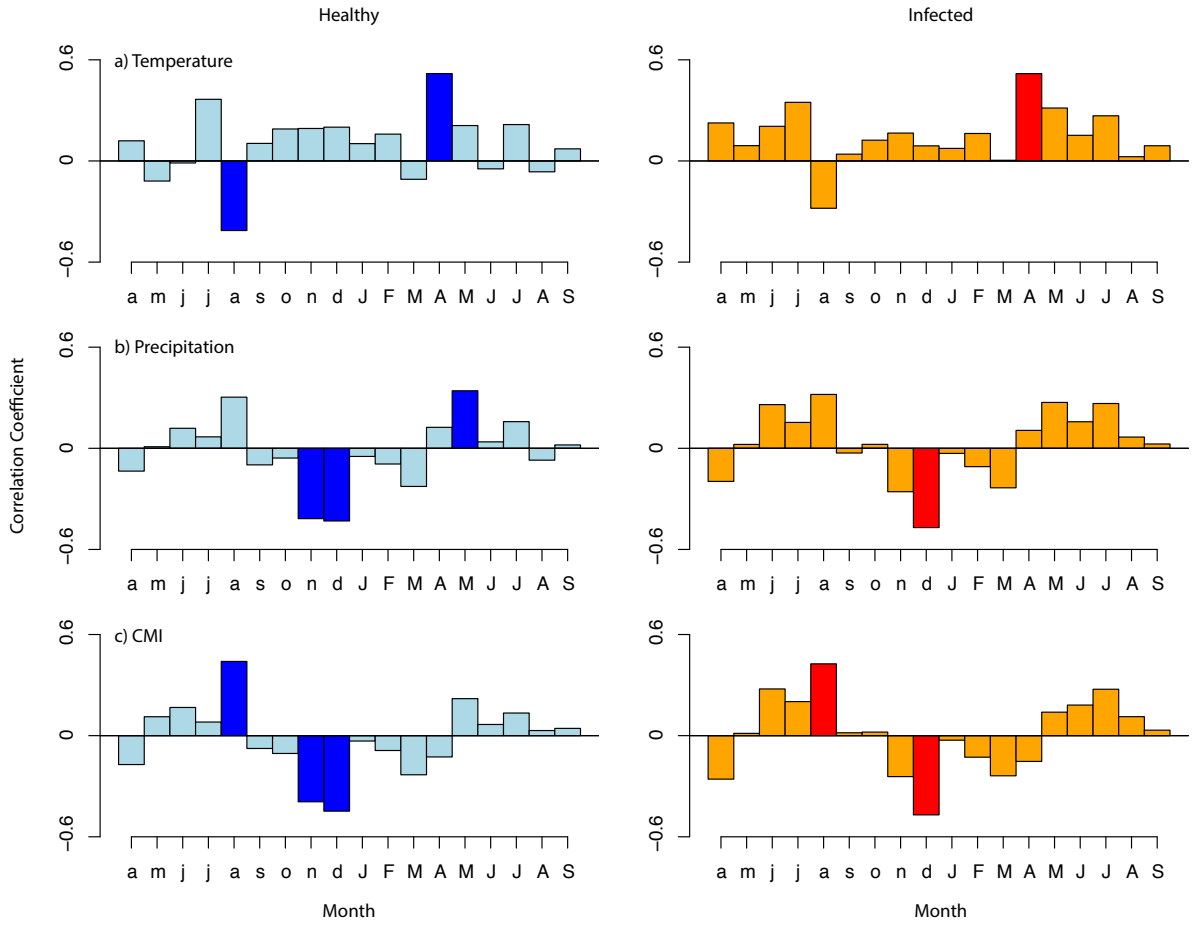

Figure 3.8: Northern region bootstrapped correlations (1954-1983) between residual master chronologies of healthy (blue) and infected (orange) trees and climate variables. The 18-month period was examined from April of the previous year to September of the current year. Lower case letters denote months of the previous year, and upper case letters denote the current year's months. The darker bars are significant at $\alpha = 0.05$.

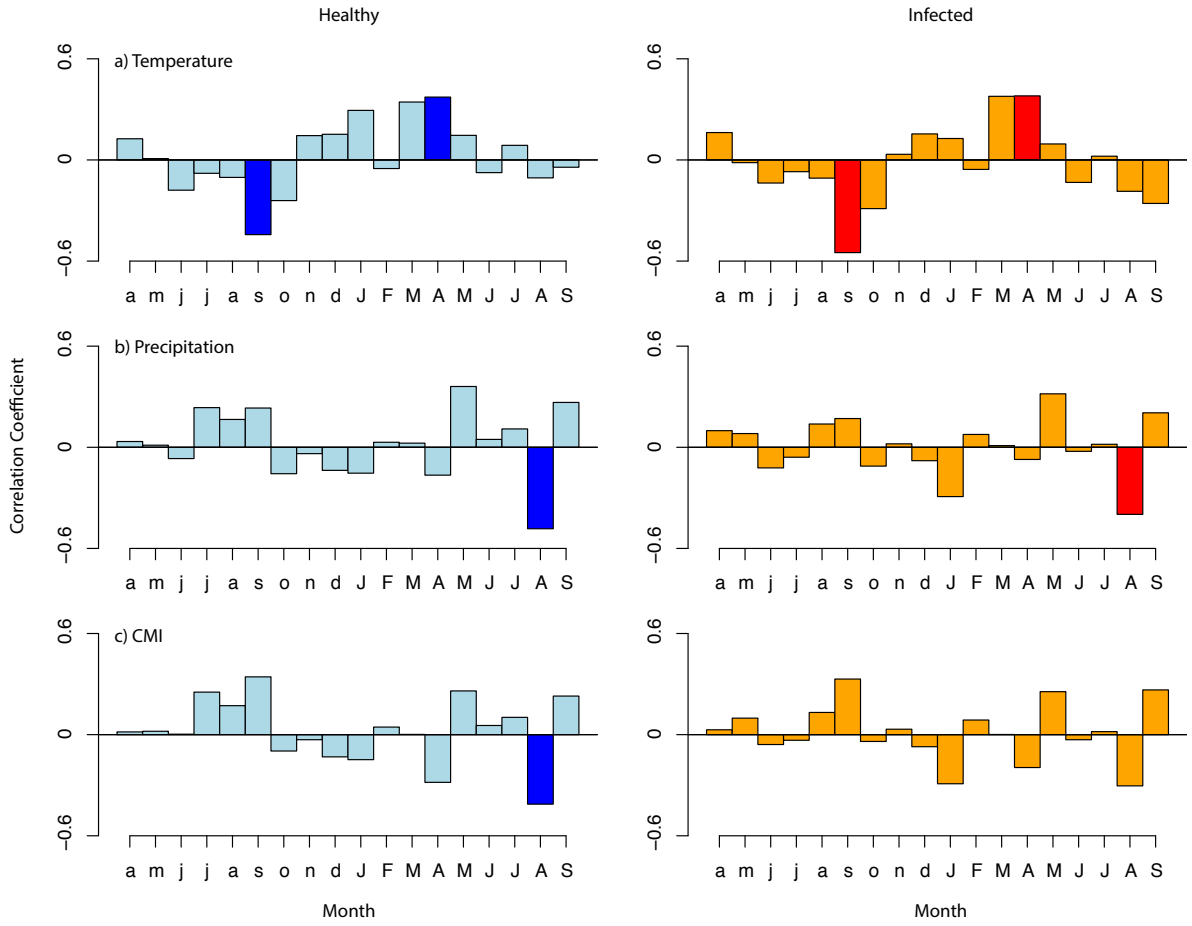

Figure 3.9: Northern region bootstrapped correlations (1984-2014) between residual master chronologies of healthy (blue) and infected (orange) trees and climate variables. The 18-month period was examined from April of the previous year to September of the current year. Lower case letters denote months of the previous year, and upper case letters denote the current year's months. The darker bars are significant at $\alpha = 0.05$.

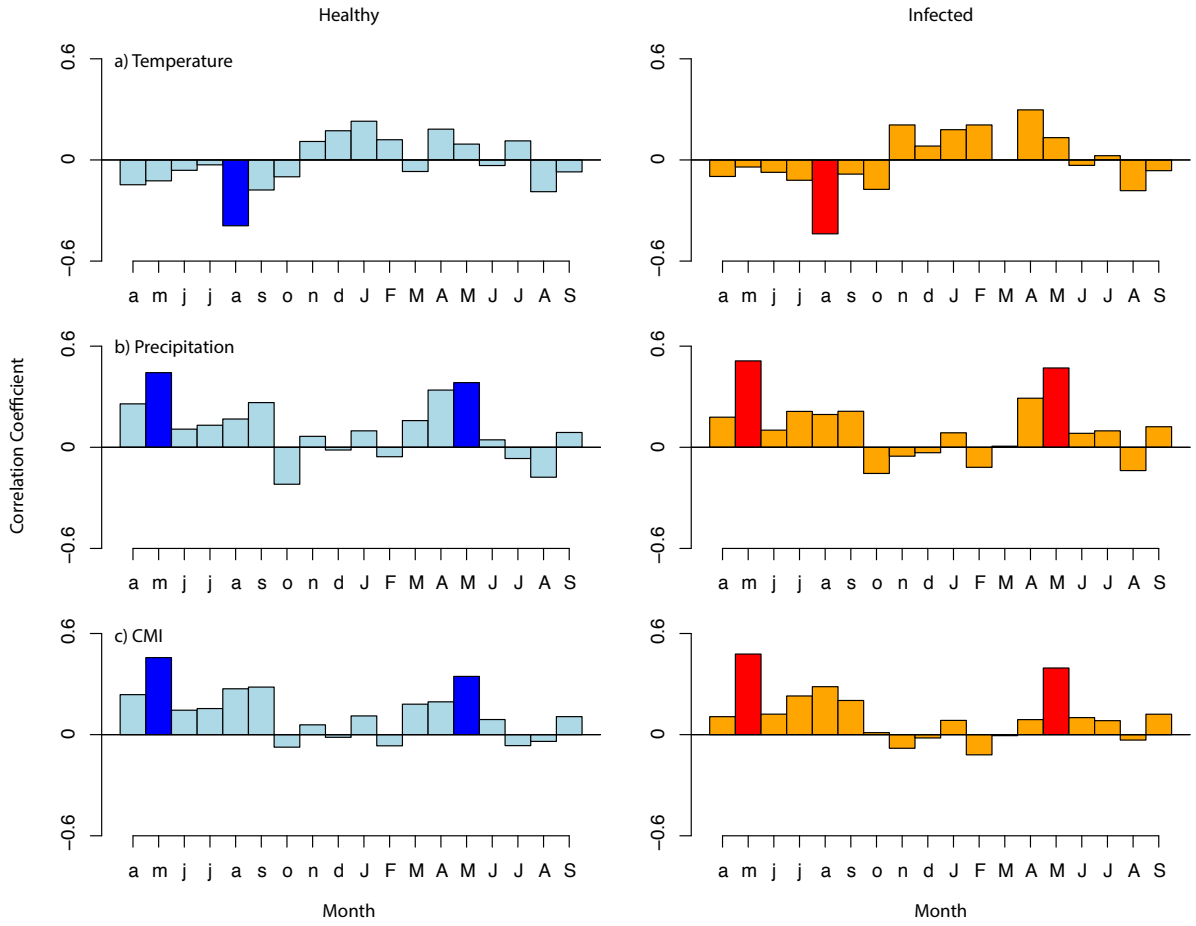

Figure 3.10: BERMS region bootstrapped correlations (1954-1983) between residual master chronologies of healthy (blue) and infected (orange) trees and climate variables. The 18-month period was examined from April of the previous year to September of the current year. Lower case letters denote months of the previous year, and upper case letters denote the current year's months. The darker bars are significant at $\alpha = 0.05$.

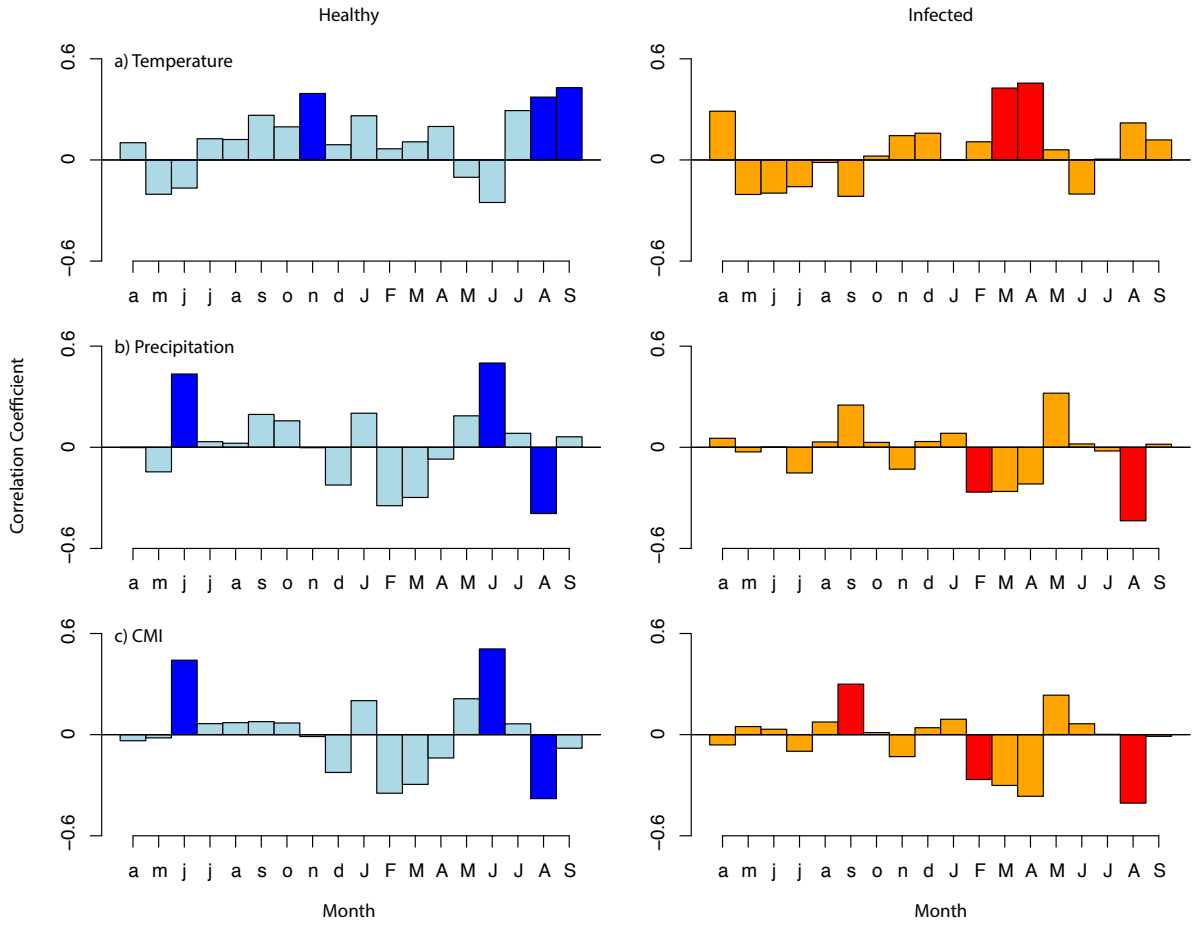

Figure 3.11: BERMS region bootstrapped correlations (1984-2014) between residual master chronologies of healthy (blue) and infected (orange) trees and climate variables. The 18-month period was examined from April of the previous year to September of the current year. Lower case letters denote months of the previous year, and upper case letters denote the current year's months. The darker bars are significant at $\alpha = 0.05$.

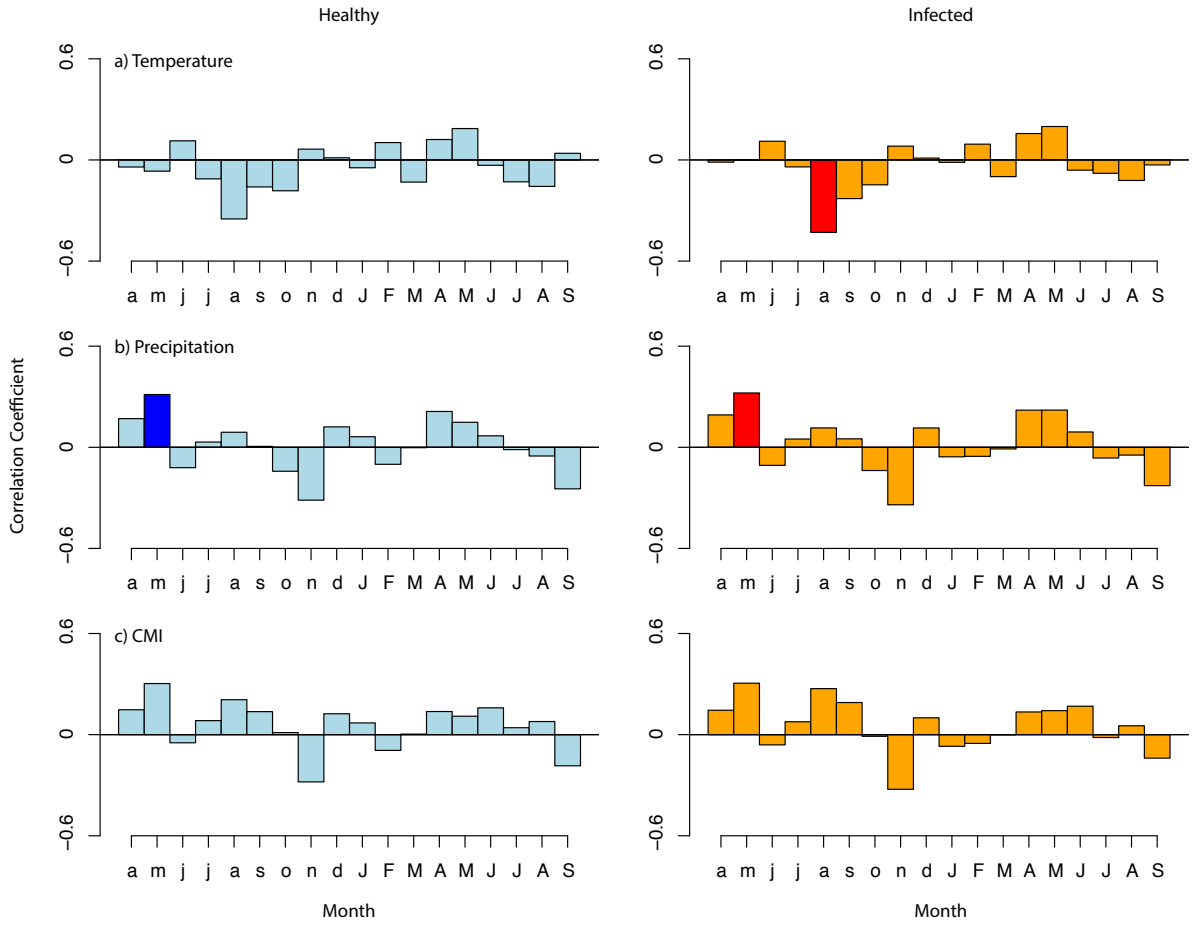

Figure 3.12: Southern region bootstrapped correlations (1954-1983) between residual master chronologies of healthy (blue) and infected (orange) trees and climate variables. The 18-month period was examined from April of the previous year to September of the current year. Lower case letters denote months of the previous year, and upper case letters denote the current year's months. The darker bars are significant at $\alpha = 0.05$.

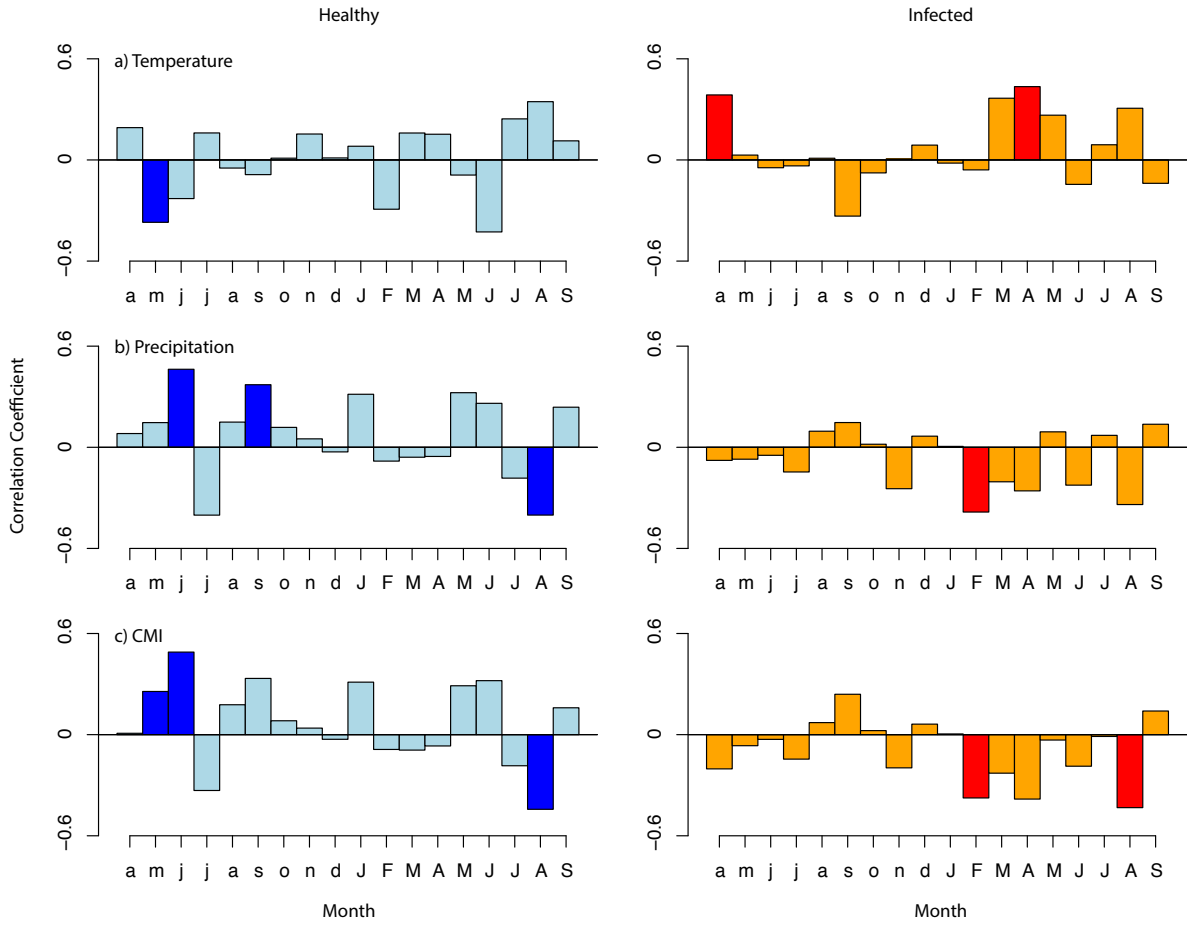

Figure 3.13: Southern region bootstrapped correlations (1984-2014) between residual master chronologies of healthy and infected trees and climate variables. The 18-month period was examined from April of the previous year to September of the current year. Lower case letters denote months of the previous year, and upper case letters denote the current year's months. The darker bars are significant at $\alpha = 0.05$.

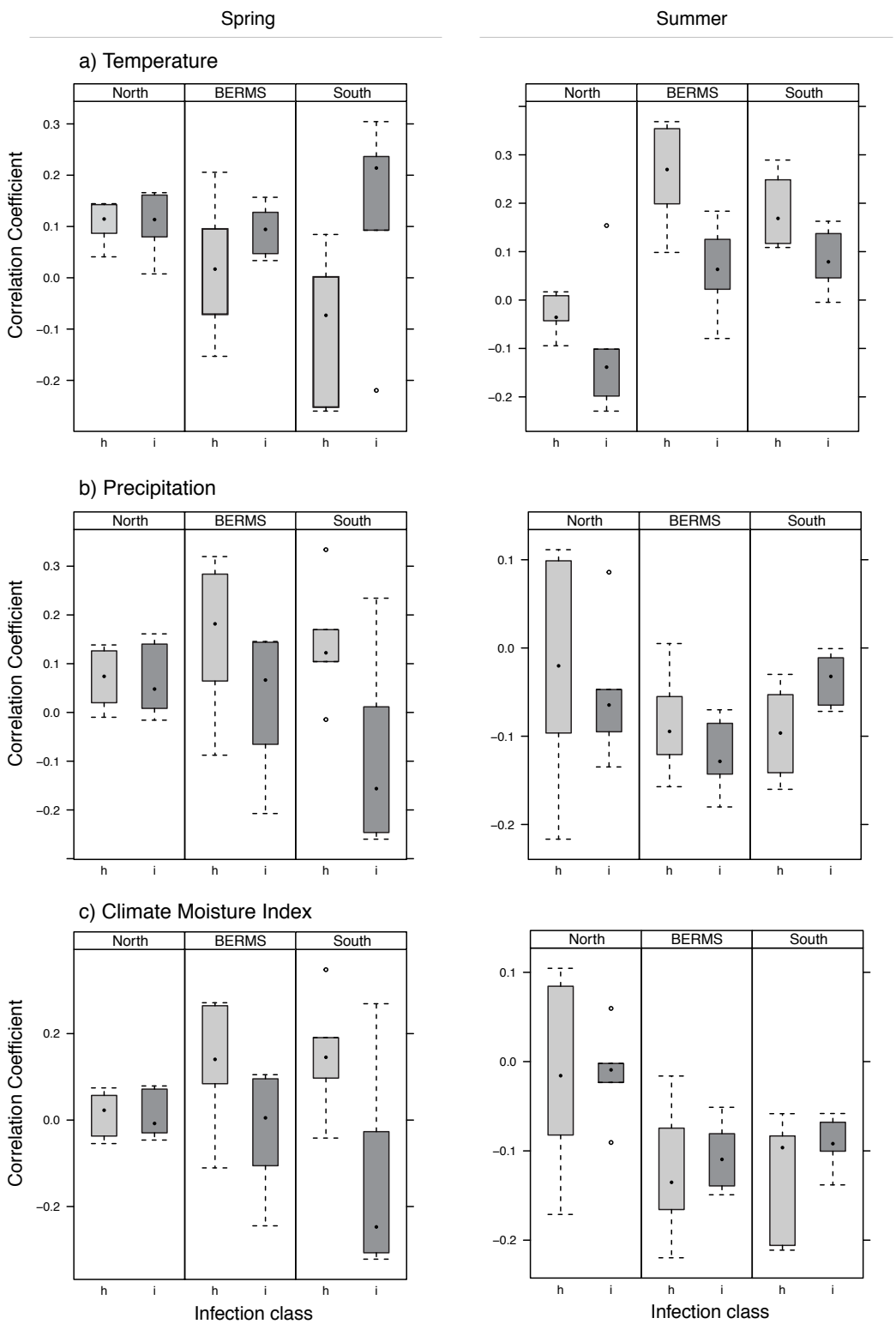

Figure 3.14: Conditional box plots showing the correlation between radial growth and the six climate variables of the current year (spring is the left column, summer is the right column) for healthy (h) and infected (i) trees in each of the three study regions.

CHAPTER 4

DISCUSSION

My first hypothesis was that DM infection would cause a decline in radial growth of infected jack pine. I found this to be the case in all study regions, where radial growth of infected trees diverged from the pattern exhibited by healthy trees, with few exceptions. Secondly, I posited that there would be a difference in the climate-radial growth relationship between healthy and infected jack pine. I observed differences in the magnitude and direction of the correlation between climate variables and radial growth, where changes were more pronounced in the southernmost regions. Thirdly, I suggested that DM would be the primary driver of these differences in the climate-growth relationship. I found that DM infection was the primary factor influencing differences in climate sensitivity for only one climate variable, summer temperature. However, DM was important for spring moisture variables, as an interaction between infection and study region showed an increasing influence of DM from North to South. Finally, I hypothesized that DM infection would interact with and exacerbate drought stress effects on jack pine in the southernmost regions of the BPE, causing an increase in sensitivity to climate variability. One of the most interesting results from this study was an interaction between DM infection and study region, with the South being the only region showing this interaction. Infected trees in the Southern region responded negatively to moisture (spring precipitation and CMI), while healthy trees responded positively. The sensitivity of infected trees to moisture was significantly altered as compared to healthy trees in this region.

4.1 Hypothesis #1 - Dwarf Mistletoe and Jack Pine Radial Growth

I observed differences in radial-growth patterns between healthy and infected chronologies across all study regions, with few exceptions. There was a decline in radial growth of severely infected trees that was not observed in healthy trees. This is consistent with the findings of several studies of other DM-host combinations in North America and Europe (Stanton 2006, Catal and Carus 2011, Sangüesa-Barreda et al. 2012, 2013, Scott and Mathiasen 2012, Logan et al. 2013). In general, as DM infection intensifies and broom abundance on the host increases, a decrease in radial growth occurs relative to healthy or non-host trees. This is due to the appropriation of resources, such as water, photosynthate, and other nutrients (Hawksworth and Wiens 1996) by the DM from the host. As infection spreads within a host tree, more brooms

develop and act as ‘nutrient sinks’. DM has been shown to create changes in the production of growth hormones (such as cytokinin), which alters apical dominance and leads to the dense broom formation (Geils and Hawksworth 2002, Logan et al. 2013). Higher transpiration in DM (compared to host tissues) (Tocher et al. 1984) increases the movement of water and nutrients to the infection sites (Hawksworth and Wiens 1996). More water and nutrients are lost from the host to the brooms than to the DM plant itself (Hawksworth and Wiens 1996). Thus, the more brooms present on a tree, the more water and nutrients are lost to the infection, and less are available for radial growth of the host tree.

I was able to visually select a divergence year where the radial growth patterns of healthy and infected chronologies began to change. Furthering this, I was also able to detect the divergence points between healthy and infected chronologies using change point detection with a broken stick model. Interestingly, the model was quite effective at determining the divergence year that I picked through visual estimation, within 5 years in most cases. The model more frequently chose an earlier year than what I could determine visually, which may indicate a threshold in the radial growth pattern that is too subtle for visual estimation. In some study regions, the broken stick model was also sensitive to the time period used. For the Northern region it worked well in both time periods for all sites, in the BERMS and Southern regions it worked well for one and not the other. This could be due to the higher mean sensitivity at BERMS and in the Southern region, where growth departures between healthy and infected trees in preceding decades may have dominated the growth patterns picked up by the model. Since the recent divergence caused by DM is often short relative to the chronology length, longer-term trends tend to dominate depending on the time period examined. Regardless, unless there was no divergence point to be found, the model was able to determine a change point for the majority of sites that was similar to my visual estimate. For some sites I could not visually determine a divergence point, and the broken stick model was consistent in its inability to detect a recent change point for these sites as well.

The divergence point is indicative of the point at which the infection became severe enough to impact radial growth. I am confident that this altered growth pattern is due to the infection by DM, and less so from environmental factors for several reasons. First, for each study region, three of the four chronology comparisons were made between healthy and infected trees growing at the same site. These trees were growing in the same environmental conditions and

experiencing the same levels of competition. While there was some variation at each site, the conditions were essentially the same for all healthy and infected trees, thus the only factor that clearly differed between healthy and infected trees was the DM. Secondly, comparisons of healthy and infected trees from different sites showed the same pattern regardless of study region. For this pattern to emerge in three different environments and not be due to the effect of DM would be very coincidental. Third, I selected the most severely infected trees to compare to healthy trees at every site. I did this to ensure that I would have the best chance to see an effect of DM on radial growth, as this trend of reduced radial growth in infected trees has been reported in other DM-host combinations (Stanton 2006, Catal and Carus 2011, Sangüesa-Barreda et al. 2012, 2013, Scott and Mathiasen 2012, Logan et al. 2013).

By detecting a divergence point, rather than simply comparing recent growth between infection groups, I am closer to being able to determine an initial infection year. Estimating the timing of initial infection is complex, as DM has a long reproductive cycle and therefore spreads slowly within a tree and through a stand. *A.americanum* is a good example, needing at minimum an average of six years from initial infection to the first seed production (Hawksworth and Wiens 1996). However, it can take up to 8 years for *A.americanum* to produce shoots after infection, and an additional one or two years before initial flowering (Hawksworth and Wiens 1996). Albeit, the lifecycle of *A.americanum* with host jack pine is shorter than with lodgepole pine, likely due to the shorter evolutionary association with jack pine (Brandt 2006). DM infection does not appear to negatively affect tree growth until many brooms are present, and the infection is classified as 'severe' (Stanton 2006, Catal and Carus 2011, Sangüesa-Barreda et al. 2012, 2013, Scott and Mathiasen 2012, Logan et al. 2013). However, some studies have reported increased radial growth in trees that were 'lightly' or 'moderately' infected (Stanton 2006, Catal and Carus 2011, Scott and Mathiasen 2012, Logan et al. 2013). Interestingly, I observed in some cases that the infected chronology had higher growth in years preceding the divergence point. Though this could be due to environmental factors, it has been suggested that this trend could be due to an increase in respiration and metabolism in infected trees when conditions are favourable to growth (Scott and Mathiasen 2012). If this is the case, further examination of a 'growth surge' prior to divergence and the climatic conditions surrounding it might be a tool for determining a point of initial infection of the tree by DM. In any case, once the decline in radial growth begins, it seems that most infected trees will die sooner than healthy trees, based on visual examination of the

chronologies, as it appears that senescence has begun. This is corroborated by an observation that within 40 years, severely infected trees had nearly all died, and did so a faster rate than healthy trees (Hawksworth et al. 2002). While I did not sample dead trees infected by DM, my results show that tree growth is declining faster in infected trees, which may suggest that mortality will occur sooner than this, and it is possible that most trees will die within two decades of infection becoming severe.

4.2 Hypothesis #2 - Climate Responses

4.2.1 Temporal

Current changes to climate in my study regions from the early (1954-1983) to recent (1984-2014) 30-year periods corroborate trends occurring in the southern boreal forest of western Canada, particularly with respect to precipitation. The dry southern forests of the western boreal have seen an increase in precipitation since the 1950's (Price et al. 2013). I observed this trend in my two southernmost regions, which increased in precipitation overall, but particularly in June. A shift in overall precipitation from less snow to more rain has also occurred, as winter temperatures have increased from the early to recent periods. Temperature increases in summer months have not been as prominent in my study regions, however future projections show increases in mean daily minimum and maximum temperatures that will likely offset any increases in future precipitation by driving higher rates of evapotranspiration (Price et al. 2013).

My results suggest that tree growth sensitivity to climate variability has changed from the earlier 30-year period (1954-1983) to the more recent period (1984-2014). Sensitivity to climate has increased in the recent 30-years, particularly in the BERMS and Southern regions. This change occurred for both healthy and infected chronologies, for all climate variables. Tree growth is more sensitive to climate when the tree is experiencing stress (Fritts 1976). Thus, it seems that increased sensitivity to climate occurring in the BERMS and Southern regions may indicate that observed changes in climate have made for a more stressful environment in recent period in these regions. Changes in sensitivity could also be a result of differential usage of resources by trees of different ages. However, the portion of the master chronology that was used for this analysis was from 1954 onward, after which point all trees were mature. It is also important to note that in the previous 30-year climate period, prior to any DM infection, trees were responding similarly to climate variability.

4.2.2 Hypothesis #3 - Dwarf mistletoe

Comparison of healthy and infected jack pine growing in the same region revealed some patterns that do not fit my hypothesis of increased sensitivity due to infection. I frequently observed infected trees to be less sensitive to climate than their healthy counterparts. It may be the case that when conditions are good for DM growth, more abundance of resources during important growth periods, infected trees show subdued responses to climate variables compared to healthy trees. Summer temperature is important for DM, as it is a key factor in late summer for pollen formation (Hawksworth and Wiens 1996), and shoot elongation (Brandt 2006). We see the relationship between ring width and summer temperature significantly altered in infected trees in all study regions. DM infected trees show lower correlations with summer temperature in every study region, rather than higher sensitivity, as we would expect. This could be due to how resources are allocated in the tree when DM is present. Tree growth may be restricted due to unequal partitioning of available resources, thus we do not see radial growth to be as sensitive to climate as compared to healthy trees.

Interestingly, DM infected trees in the BERMS and Southern regions showed positive correlations with early spring temperature (March and April) that were not prominent with healthy trees. Warm temperatures positively influenced tree growth in early spring, prior to the onset of the growing season. This is likely due to thawing and warming of the soil with higher temperatures, thus when trees break dormancy they are able to begin growing right away, and are not impeded by DM at this time. Early spring relates to the onset of flowering in DM, and *A. americanum* is one of the earliest DM species to initiate flowering, which occurs in March or April (Hawksworth and Wiens 1996). It is possible that the DM is not actively stealing water and nutrients at this time, as its pollen was produced in the late summer of the previous year, and it awaits pollinators in the spring. Perhaps when the parasite is not using available resources the tree is able to reallocate them to its own growth processes, which may help to explain why we do not see the same strong correlation in healthy trees. This is one example of infected trees showing an increase in sensitivity to a climate variable.

The moisture variables, precipitation and CMI, in the BERMS region had very similar relationships to ring width. This is an expected result, as CMI is an index of moisture that is derived from the balance between precipitation and potential evapotranspiration, which is driven by temperature (Hogg 1994, 1997). Higher values for CMI are indicative of higher precipitation.

Differences between healthy and infected trees occurred for previous and current-June, where healthy trees were positively correlated and infected trees had a near zero correlation. This point in the year corresponds to DM seed production after pollination and preparation for dispersal (Brandt 2006). It is possible that in June as DM prepares for dispersal, a large portion of the available water is allocated to the parasite and as a result trees are not physiologically able to respond to increased moisture. It is possible that there is, effectively, little moisture available to the tree, thus it does not have increased growth, as we see with healthy trees. June had the highest amount of precipitation in the BERMS and Southern regions from 1984-2014, and only slightly negative CMI values. It is the only month for which the CMI value in the Northern region is more negative than the BERMS and Southern regions.

Relationships between ring width and moisture variables in the Southern region change from largely positive in healthy trees, to close to zero or negative for infected trees. The Southern region has the highest temperatures, as well as the most negative CMI values during the spring and summer months, with the exception of June, of the three regions. However, temperature and precipitation in the Southern region from 1984-2014 have been very similar to that of the BERMS region. In the Southern region infected trees showed either no response, or a negative response to increasing moisture. This is similar to our observations from the BERMS region, except that positive responses to June moisture were consistently negative in infected trees in the Southern region. In fact, the majority of correlations with moisture variables were negative in the South, where they were largely positive for healthy trees. While we can somewhat explain a lack of correlation as observed in the BERMS region, negative correlations to moisture in a region with the most negative moisture balance is counterintuitive.

Trees that are limited by moisture availability should respond positively to an addition of moisture (Fritts 1976), which we see in healthy trees. In addition to this, the South was the only region for which there was a significant interaction between DM infection and location in the regional moisture gradient in my GLM. The interaction essentially told us what we observed above, that the correlations of healthy and infected trees to spring moisture variables were very similar in the Northern region, and diverged from North to South. They differed significantly in the South, with healthy trees having positive, and infected trees having negative correlations. The interaction between infection and study area would suggest that DM is having an inordinate

impact on tree-climate sensitivity in the Southern region. This might be evidence to support my hypothesis that drought stress effects on jack pine may be exacerbated by interactions with DM.

4.3 Hypothesis #4 - Dwarf Mistletoe and Drought

I found some evidence that drought stress, or moisture limitation, interacts with DM infection to alter tree responses to climate. First of all, there were differing responses of trees to climate, and particularly moisture variables in the Northern compared to the BERMS and Southern regions, while these two southernmost regions were very similar to one another. If the impact of DM on tree-growth sensitivity to climate were strictly due to the parasite, then we would expect to see no differences between the three regions. The BERMS and Southern regions were both drier than the North for most of the year. Thus, water availability seems to be an important factor governing the impact of DM infection on radial growth in infected trees. Normally, when water becomes available in a dry environment, a tree will respond by growing more, as we can see in the climate relationship in healthy trees. If infected trees are responding in the opposite way, what is the DM doing to the tree to cause a decrease in radial growth when moisture becomes available? We can try to answer this with knowledge from other DM-host combinations. The first factor is likely the host condition, when the tree has access to water, the water stress is lessened and the DM is able to grow well again (Bickford et al. 2005). The condition of the host tree has been shown to affect the performance of DM (Bickford et al. 2005). When there are more available resources, the tree will take up more resources, and the DM will thus have access to more resources. Secondly, high precipitation on a sandy soil, such as that found in the BPE, will be rapidly drained. Thus, it is unlikely that all water that falls as precipitation is actually available to the trees and we may see negative correlations with higher precipitation because total precipitation recorded is not necessarily equivalent to biologically available moisture. Third, Reblin et al. (2006) showed that witches' brooms caused by eastern dwarf mistletoe (*Arceuthobium pusillum*) are effectively nutrient sinks, because photosynthetic ability is weak in broomed branches in white spruce (*Picea glauca*). DM draws water (and nutrients) to infected branches, where high transpiration rates will lead to water loss from the brooms (Hawksworth and Wiens 1996). Higher levels of cytokinin in the needles of white spruce infected with eastern dwarf mistletoe not only lead to the dense branching characteristic of DM infection, but also draw water and nutrients to these sites, making these brooms nutrient sinks

(Logan et al. 2013). Thus the greater the proportion of branches that are witches' brooms, the greater the negative impacts on tree growth. We can reason that the reduced radial growth in severely infected trees is a direct result of the disproportionate division of resources to the high number of brooms. Trees are essentially handicapped in a situation where they should be taking advantage of resource availability.

Despite the fact that more precipitation fell in June in the recent 30-year period, tree growth is declining and the climate response is altered in infected trees. The effect of DM on these trees could be compared to the effect that increasingly high temperatures would have on trees, offsetting any potential benefits of higher precipitation. Similar effects have been described in temperature limited environments, where trees show insensitivity to increasing temperatures where one would expect increased sensitivity (D'Arrigo et al. 2008). This is known as the 'divergence effect', which occurs when drought stress induced by temperature in northern environments prevents trees from responding when temperature increases (D'Arrigo et al. 2008). Perhaps DM creates this type of response in infected trees, where the evapotranspiration rate is so great as a result of broom abundance that trees do not show growth sensitivity to moisture input. This response of DM infected trees might provide a window into the future where increasing temperatures are expected to create evaporative demand such that the expected increase in precipitation will not be enough to sustain tree growth, and ultimately lead to greater tree mortality.

4.4 Potential Implications for Forest Management

I have observed signs of decreased productivity as a reduction of annual growth increments of infected jack pine in all studied regions of the BPE. However, only infected trees in the southernmost regions show changes in how they respond to climate variability, suggesting additional effects of DM on tree physiological processes. Studies of DM from both North America and Europe have shown that drought events can be triggers for growth decline and mortality infected host trees (Sangüesa-Barreda et al. 2012, 2013, Scott and Mathiasen 2012). Mortality rates of infected trees are often the highest following drought periods (Hawksworth and Wiens 1996). Trees in the southernmost regions of the boreal forest that have altered physiological responses to climate may be weaker and more susceptible to events that trigger mortality. With increases in frequency and severity of drought events expected for western

Canada (Peng et al. 2011, Price et al. 2013), there is the possibility of widespread mortality of infected jack pine in the southern boreal forest under future climate. DM infection as it interacts with drought stress in the southern boreal forest may be a mechanism of forest contraction in the future.

Secondary or tertiary disturbances or stressors on DM infected jack pine could further impact the persistence of the species in the dry southern boreal forest. While both healthy and infected trees are susceptible to insect attack, infected trees may provide conditions that may either dampen or compound the effects of these secondary stressors. DM infection has been shown to both increase and decrease susceptibility to insect attack, depending on the host-parasite combination (Hawksworth and Wiens 1996). However, there is no work to suggest how DM infection will interact with BPE pests, such as jack pine budworm. Regardless, infected trees are weakened such that insect attack would likely result in an inability of the tree to recover and speed up mortality (Hawksworth and Wiens 1996).

It will be important to limit the spread of DM in these southern regions. Keeping healthy, seed bearing trees growing in the south could be important, as perhaps these trees are better adapted to the dry conditions. In the absence of infection by DM, these trees may be a solution to help mitigate the issues associated with the northward advance of a drier climate. Planting the seeds of jack pine from the southernmost regions of the boreal forest in the more northern regions may give the species a helping hand to cope with the coming changes. Seeds from DM infected trees may not be viable, so it will be important to protect some southern stands from infestation.

4.5 Other Interacting Disturbances

4.5.1 Dwarf mistletoe and fire

Fire disturbance both controls and enables DM perpetuation on the landscape. Fire is the most effective control of DM, as burning will kill DM and sterilize it within a stand, and fire suppression may be a contributing factor to the spread of DM (Kipfmueller and Baker 1998). Fire also perpetuates DM susceptible species, such as jack pine, which typically recolonize after fire. This benefits DM should any infected trees be left behind to re-infect a new generation of host trees (Kipfmueller and Baker 1998). Thus, in order to truly control DM populations, fire needs to be large enough to kill all infected trees in an area. Furthermore, DM can lead to fuel loading in the forest understory and canopy through excess litter accumulation and fallen brooms

(Zimmerman and Laven 1984). Brooms on trees may also act as a conduit for fire to rise into the upper canopy, and DM makes tree tissue more flammable, by increasing resin production (Zimmerman and Laven 1984, Hawksworth et al. 2002). Complicating the issue is expected changes to the climate, which may impact the fire regime in the southern boreal forest. Drought is expected to become more frequent and severe as climate change impacts this region, which creates conditions conducive to fire (Price et al. 2013). If fire occurrence increases such that the forest burns before jack pine can reach maturity, the trees may die before they are old enough to produce seeds. In open stands jack pine will mature and begin to flower in five to ten years, but in a closed canopy flowering is delayed (Rudolf and Laidly 2004). Additionally, studies of other DM-host combinations have shown that brooms on infected trees often do not produce cones, and those that do, have low seed viability (Geils and Hawksworth 2002). Jack pine produces serotinous cones, which are cones that open when exposed to high temperatures, commonly from fire (Rudolf and Laidly 2004). This regeneration strategy may collapse should seed production be reduced or seeds be unviable, and may alter which species recolonize an area after fire. A loss of natural recruitment of jack pine may be a contributing mechanism to fragmentation of the boreal forest at its southern edge. Fire may be effective in controlling DM in the future, but this may occur partially through loss of jack pine as a host in the BPE. This may initiate a transition to other shade intolerant species, such as aspen (*Populus tremuloides*), which are also widely distributed in North America and commonly colonize after fire (Howard 1996).

4.5.2 Dwarf mistletoe and anthropogenic disturbance

I observed a high degree of human disturbance in DM infected areas, though I did not measure this empirically. In general, healthy trees were more frequently located in closed canopy forested areas away from roads, whereas infected and mixed sites were more frequently located at the edge of a forest, near logging roads, cut blocks, or former man made structures. One possible explanation for this is that low light represses shoot production of DM (Hawksworth et al. 2002). In a closed canopy forest, if DM is present, it will not grow as quickly, and intensification and spread of the parasite averages 0.3-0.6 m per year may be slowed as well. Conversely, in uneven aged, or open stands with variable canopy density and height, there is more area for seed interception the spread and seed dispersal can be as fast as 9.0 -15 m per year (Hawksworth and Wiens 1996). If trees are removed for building roads, logging, etc., openings are created in the

canopy, and more light is able to enter. If low light represses growth, then input of more light would allow DM to grow more abundantly. Additionally, canopy openings could allow DM seeds to disperse longer distances, potentially up to 20 m or further in windy conditions (Hawksworth and Wiens 1996, Saskatchewan Ministry of Environment 2010). This could allow for more rapid spread through the canopy and infection of younger pines regenerating in the understory or in nearby openings. Frequently infected trees are left standing in a logged area as they are non-marketable and, therefore, not desired by industry (Rory McIntosh 2016, personal communication). However, leaving infected trees to infect a new generation of pines will lead to a generation of severely stunted trees that provide no value to industry. Removing any infected trees, thinning broomed branches, or controlling DM spread through some chemical application would be beneficial to industry by preventing the contamination of a new generation of merchantable jack pine.

CHAPTER 5

CONCLUSIONS

5.1 Summary

DM causes a decline in radial-growth of severely infected jack pine in all study regions across the BPE ecozone in Saskatchewan. Reductions in radial growth of jack pine occur when the infection is 'severe', but it is not clear at what stage of infection this occurs. However, despite the change in radial-growth patterns between healthy and infected trees, there were few changes to the growth-climate relationship in infected trees. The only climate variable for which healthy and infected trees differed across all study regions in the BPE was correlation with summer temperature. This was the only variable for which DM infection appeared to be the primary driver of differences in the correlation with climate. This suggests that warmer summer temperature is important for DM across the BPE, resulting in reduced radial growth of infected trees when temperatures are higher. Warmer temperatures are associated with improved DM performance, and both pollen production and shoot elongation occur in the late summer (Hawksworth and Wiens 1996). Thus, increases in future temperatures in the BPE may slow the growth of infected jack pine. There was also an interaction between DM infection and the Southern region in relation to spring precipitation and spring CMI. This helps support the hypothesis that DM and moisture stress interact to impair jack pine radial-growth, as the South is the driest study region across the BPE (Hogg 1994, 1997, Hogg and Hurdle 1995). The interaction indicated that infected trees were growing less when moisture (precipitation or CMI) was increased. This means that despite this resource becoming more abundant, there is not enough for both DM and the tree to utilize. If drought conditions occur more frequently in the future (Price et al. 2013), infected trees may become more stressed and additionally unable to make use of moisture when it becomes available. As a result, infected trees in these drier areas will likely die quicker than infected trees elsewhere in the BPE.

In general, these results suggest that DM infected jack pine will be negatively affected by the parasite throughout the BPE as the climate changes. Warmer temperatures may increase DM success, while slowing radial growth of the host. Trees in the southernmost portions of the BPE will likely have impaired growth capabilities as a result of DM infection, in addition to the stress of increased moisture limitations due to climate change. The probable outcome of this will be

extensive mortality of jack pine at the southern edge of the boreal forest in Saskatchewan, and the Prairie Provinces. This would mean loss of jack pine in the remnant island forests, and potential fragmentation at the southern edge of the continuous boreal forest. The effects of DM on jack pine we observe in the Southern boreal forest may be indicative of what can be expected as current climatic conditions of the Aspen Parkland-Boreal Transition ecoregion boundary shifts northward (Hogg 1994, 1997, Hogg and Hurdle 1995). This poses a threat to the forestry industry in Saskatchewan and the other Prairie Provinces. Sustainable forest management requires long-term planning and must be adaptive and take into account climate change and how it impacts and interacts with biotic disturbances. Understanding how biotic disturbances, such as DM, are affected by climate change can help us find ways to mitigate tree mortality. This study helps to improve our knowledge of the DM-jack pine parasite-host relationship, minimize the uncertainty and improve forest management in the western Canadian boreal forest for the future sustainable use of our forest resources.

5.2 Areas for future research

Dwarf mistletoes are one of the least studied organisms with respect to climate change and forest disturbance (Weed et al. 2013). To my knowledge this study is the first to address potential impacts of climate change induced drought stress and DM in the Saskatchewan boreal forest. However, there are many gaps in our understanding of the jack pine – DM system that remain to be filled. It is clear that not all host-parasite combinations are created equal, and generalizations from one system to another are not always reliable. For example, the relationship between lodgepole pine and DM in British Columbia, Alberta and Manitoba has been used to develop guidelines and policies to inform management of DM in jack pine forest in Saskatchewan (McIntosh 2004, Saskatchewan Ministry of Environment 2010). However, differences in the specific host-parasite system can exist, such as the differing length of the DM lifecycle (Brandt 2006), thus it becomes important to further investigate specific relationships. There are several areas for potential future research for jack pine infected with DM in Saskatchewan:

1) assessing the production of cones and viability of seeds from infected branches, to determine whether jack pine reproduction is impaired by the parasite;

2) assessing the influence of anthropogenic disturbance on the spread of DM in the southern boreal forest, in order to inform forestry practices and limit the spread of DM;
3) assessing the potential for drought resistance in jack pine growing at its southern range limits, and whether cultivating seedlings to regenerate stands is a viable solution as the climate changes; and
4) further examining the onset and progression of DM infection in the radial-growth patterns of jack pine.

REFERENCES

Acton, D.F., Padbury, G.A., and Stushnoff, C.T. 1998. Boreal Plain Ecozone. *In* The Ecoregions of Saskatchewan. Canadian Plains Research Centre/ Saskatchewan Environment and Resource Management, Regina, SK. pp. 73–75.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. **259**(4): 660–684. doi:10.1016/j.foreco.2009.09.001.

Baker, F.A. 1992. Impact of Dwarf Mistletoe on Jack Pine Forests in Manitoba. Plant Dis. **76**(12): 1256. doi:10.1094/PD-76-1256.

Barr, A.G., van der Kamp, G., Black, T.A., McCaughey, J.H., and Nesic, Z. 2012. Energy balance closure at the BERMS flux towers in relation to the water balance of the White Gull Creek watershed 1999–2009. Agric. For. Meteorol. **153**: 3–13. doi:10.1016/j.agrformet.2011.05.017.

Bickford, C.P., Kolb, T.E., and Geils, B.W. 2005. Host Physiological Condition Regulates Parasitic Plant Performance: *Arceuthobium vaginatum* Subsp. *cryptopodum* on *Pinus ponderosa*. Oecologia **146**(2): 179–189.

Biondi, F., and Waikul, K. 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Comput. Geosci. **30**: 303–311.

Brandt, J.P. 2006. Life cycle of *Arceuthobium americanum* on *Pinus banksiana* based on inoculations in Edmonton, Alberta. Can. J. For. Res. **36**(4): 1006–1016. doi:10.1139/x05-288.

Brandt, J.P., Brett, R.D., Knowles, K.R., and Sproule, A. 1998. Distribution of severe dwarf mistletoe damage in west-central Canada. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta.

Brandt, J.P., Flannigan, M.D., Maynard, D.G., Thompson, I.D., and Volney, W.J.A. 2013. An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues. Environ. Rev. **21**(4): 207–226. doi:10.1139/er-2013-0040.

Brooks, J.R., Flanagan, L.B., and Ehleringer, J.R. 1998. Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. Can. J. For. Res. **28**(4): 524–533. doi:10.1139/x98-018.

Bunn, A.G. 2008. A dendrochronology program library in R (dplR). Dendrochronologia **26**(2): 115–124. doi:10.1016/j.dendro.2008.01.002.

Burnham, K.P., Anderson, D.R., and Huyvaert, K.P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. **65**(1): 23–35. doi:10.1007/s00265-010-1029-6.

Carroll, A.L., Taylor, S.W., Régnière, J., and Safranyik, L. 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. *In* Pages 223-232 in TL Shore et al.(eds) Mountain Pine Beetle Symposium: Challenges and Solutions, Oct. 30-31, 2003. Kelowna BC. Natural Resources Canada, Infromation Report BC-X-399, Victoria. Available from http://digitalcommons.usu.edu/barkbeetles/195/ [accessed 30 March 2016].

Catal, Y., and Carus, S. 2011. Effect of pine mistletoe on radial growth of Crimean pine (*Pinus nigra*) in Turkey. J. Environ. Biol. Acad. Environ. Biol. India **32**(3): 263–270.

Chambers, J.M., and Hastie, T.J. 1992. Statistical Models in S. Wadsworth & Brooks/Cole.

Cook, E.R. 1985. A time-series analysis approach to tree-ring standardization. University of Arizona, Tuscon, AZ.

Crawley, M.J. 2007. The R Book. Wiley & Sons, Chichester, West Sussex, England.

D'Arrigo, R., Wilson, R., Liepert, B., and Cherubini, P. 2008. On the "Divergence Problem" in Northern Forests: A review of the tree-ring evidence and possible causes. Glob. Planet. Change **60**(3–4): 289–305. doi:10.1016/j.gloplacha.2007.03.004.

Environment Canada. 2015. National Climate Data and Information Archive Meteorlogical Service of Canada. Available from http://climate.weather.gc.ca//index_e.html#access [accessed 23 November 2015].

Epp, B., and Tardif, J.C. 2004. Effects of lodgepole pine dwarf mistletoe, *Arceuthobium americanum*, on jack pine, *Pinus banksiana*, growth in Manitoba. Can. Field-Nat. **118**(4): 595–601.

Farrar, J.L. 1995. Group 3 (Pines): Jack Pine. *In* Trees of the Northern United States and Canada. Iowa State Press, IA. pp. 58–59.

Fritts, H.C. 1976. Tree Rings and Climate. Academic Press, University of California.

Geils, B.W., and Hawksworth, F.G. 2002. Chapter 5: Damage, Effects, and Importance of Dwarf Mistletoes. *In* Mistletoes of North American Conifers. USDA Forest Service Gen. Tech. Rep. pp. 57–65.

Grissino-Mayer, H.D. 2001. Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA. Tree-Ring Res. Available from http://arizona.openrepository.com/arizona/handle/10150/251654 [accessed 3 October 2014].

Hawksworth, F.G. 1965. Life tables for two species of dwarf mistletoe. I. Seed dispersal, interception, and movement. For. Sci. **11**: 142–151.

Hawksworth, F.G. 1977. The 6-class dwarf mistletoe rating system. Gen. Tech. Rep., United States Forest Service.

Hawksworth, F.G., and Wiens, D. 1996. Dwarf Mistletoes: Biology, Pathology, and Systematics. United States Department of Agriculture, Forest Service.

Hawksworth, F.G., Wiens, D., and Geils, B.W. 2002. Chapter 4: Arceuthobium in North America. *In* Mistletoes of North American Conifers. USDA Forest Service Gen. Tech. Rep. pp. 29–56.

Hiratsuka, Y., Langor, D.W., and Crane. 2004. Field guide to forest insects and diseases of the prairie provinces. *In* 2nd edition. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta.

Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. Can. J. For. Res. **24**: 1835–1845.

Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agric. For. Meteorol. **84**(1–2): 115–122. doi:10.1016/S0168-1923(96)02380-5.

Hogg, E.H., and Bernier, P.Y. 2005. Climate change impacts on drought-prone forests in western Canada. For. Chron. **81**(5): 675–682. doi:10.5558/tfc81675-5.

Hogg, E.H., Brandt, J.P., and Michaelian, M. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can. J. For. Res. **38**(6): 1373–1384. doi:10.1139/X08-001.

Hogg, E.H., and Hurdle, P.A. 1995. The aspen parkland in western Canada: A dry-climate analogue for the future boreal forest? Water. Air. Soil Pollut. **82**(1-2): 391–400. doi:10.1007/BF01182849.

Hogg, E.H. (Ted), and Brandt, J.P. 2002. Growth and dieback of Aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Can. J. For. Res.-Rev. Can. Rech. For. - CAN J For. RES **32**(5): 823–832. doi:10.1139/x01-152.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. **43**: 69–75.

Hosie, R.C. 1990. The Pines: Jack Pine. *In* Native Trees of Canada, 8th edition. Fitzhenry and Whiteside Ltd, Ontario, Canada. pp. 50–51.

Howard, J.L. 1996. Populus tremuloides. *In* Fire Effects Information System [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Available from http://www.fs.fed.us/database/feis/ [accessed 25 April 2016].

Johnston, M., Williamson, T., Wheaton, E., Wittrock, V., Nelson, H., Hesseln, H., Vandamme, L., Pittman, J., and Lebel, M. 2008. Climate Change Adaptive Capacity of Forestry Stakeholders in the Boreal Plains Ecozone. Saskatchewan Research Council.

Kipfmueller, K.F., and Baker, W.L. 1998. Fires and dwarf mistletoe in a Rocky Mountain lodgepole pine ecosystem. For. Ecol. Manag. **108**(1–2): 77–84. doi:10.1016/S0378-1127(98)00217-5.

Little, E.L.J. 1971. Conifers and important hardwoods. *In* Atlas of United States trees. U.S. Department of Agriculture Miscellaneous Publication 1146. p. 9.

Logan, B.A., Reblin, J.S., Zonana, D.M., Dunlavey, R.F., Hricko, C.R., Hall, A.W., Schmiege, S.C., Butschek, R.A., Duran, K.L., Emery, R.J.N., Kurepin, L.V., Lewis, J.D., Pharis, R.P., Phillips, N.G., and Tissue, D.T. 2013. Impact of eastern dwarf mistletoe (*Arceuthobium pusillum*) on host white spruce (*Picea glauca*) development, growth and performance across multiple scales. Physiol. Plant. **147**(4): 502–513. doi:10.1111/j.1399-3054.2012.01681.x.

Mamet, S.D., Chun, K.P., Metsaranta, J.M., Barr, A.G., and Johnstone, J.F. 2015. Tree rings provide early warning signals of jack pine mortality across a moisture gradient in the southern boreal forest. Environ. Res. Lett. **10**(8): 084021. doi:10.1088/1748-9326/10/8/084021.

Mathiasen, R.L., Nickrent, D.L., Shaw, D.C., and Watson, D.M. 2008. Mistletoes: Pathology, Systematics, Ecology, and Management. Plant Dis. **92**(7): 988–1006. doi:10.1094/PDIS-92-7-0988.

McIntosh, R.L. 2004. Dwarf Mistletoe Ecology and Management. Forest Service, Saskatchewan Environment.

McLaughlan, M.., Wright, R.., and Jiricka, R.D. 2010. Field Guide to the Ecosites of Saskatchewan's Provincial Forests. Saskatchewan Ministry of Environment, Forest Service, Prince Albert, SK.

Moody, B.H., and Amirault, P.A. 1992. Impacts of major pest on forest growth and yield in the prairie provinces and the Northwest Territories: a literature review. Northern Forest Research Centre, Edmonton, Alberta.

Natural Resources Canada. 2014. National Forest Pest Strategy Information System. Natural Resources Canada, Canadian Forest Service, Atlantic Forestry Centre, Fredericton, NB. Available from https://afc-fr.cfsnet.nfis.org/NFPS-SNLRF/.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., and Zhou, X. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nat. Clim. Change **1**(9): 467–471. doi:10.1038/nclimate1293.

Piirto, D.., Crews, D.., and Troxell, H.E. 1974. The effects of dwarf mistletoe on the wood properties of lodgepole pine. Wood Fibre **6**: 26–35.

Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M., McKenney, D.W., Pedlar, J.H., Stratton, T., Sturrock, R.N., Thompson, I.D., Trofymow, J.A., and Venier, L.A. 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems [1]. Environ. Rev. **21**(4): 322–365. doi:10.1139/er-2013-0042.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/.

Reblin, J.S., Logan, B.A., and Tissue, D.T. 2006. Impact of eastern dwarf mistletoe (*Arceuthobium pusillum*) infection on needles of red (*Picea rubens*) and white spruce (*Picea glauca*): oxygen exchange, morphology, and composition. Tree Physiol. **26**: 1325–1332.

Régnière, J., and St-Amant, R. 2007. Stochastic simulation of daily air temperature and precipitation from monhtly normals in North America north of Mexico. Int. J. Biometeorol. **51**: 415–430.

Régnière, J., St-Amant, R., and Béchard, A. 2014. BioSIM 10 User's Manual. Information Report, Natural Resources Canada, Canadian Forest Service, Laurentian Forstry Centre.

Richardson, D.M. (*Editor*). 1998. Pine Diseases: dwarf mistletoe. *In* Ecology and Biogeography of Pinus. Cambridge University Press, UK. pp. 382–384.

Rudolf, T.D., and Laidly, P.R. 2004. Jack Pine (*Pinus banksiana*). *In* Silvics Manual Volume 1: Conifers. US Forest Service. p. 32.

Safranyik, L., and Carroll, A.L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *In* The Mountain Pine Beetle: Synthesis of biology, management, and impacts on lodgepole pine. *Edited by* L. Safranyik and B. Wilson. pp. 3–66.

Sakamoto, Y., Ishiguro, M., and Kitagawa, G. 1986. Akaike Information Criterion Statistics. D. Reidel Pubishing Company.

Sangüesa-Barreda, G., Linares, J.C., and Camarero, J.J. 2012. Mistletoe effects on Scots pine decline following drought events: insights from within-tree spatial patterns, growth and carbohydrates. Tree Physiol. **32**(5): 585–598. doi:10.1093/treephys/tps031.

Sangüesa-Barreda, G., Linares, J.C., and Julio Camarero, J. 2013. Drought and mistletoe reduce growth and water-use efficiency of Scots pine. For. Ecol. Manag. **296**: 64–73. doi:10.1016/j.foreco.2013.01.028.

Saskatchewan Ministry of Environment. 2010. Forest Pest Fact Sheet: Lodgepole Pine Dwarf Mistletoe, (*Arceuthobium americanum*).

Schwarz, C.J. 2015. Regression - hockey sticks, broken sticks, piecewise, change points. *In* Course Notes for Beginning and Intermediate Statstics. Available from http://www.stat.sfu.ca/~cschwarz/CourseNotes [accessed 1 February 2016].

Scott, J.M., and Mathiasen, R.L. 2012. Assessing Growth and Mortality of Bristlecone Pine Infected by Dwarf Mistletoe Using Dendrochronology. For. Sci. **58**(4): 366–376. doi:10.5849/forsci.10-142.

Speer, J.H. 2010. Field and Laboratory Methods. *In* Fundamentals of Tree-ring Research. University of Arizona Press, AZ. pp. 72–105.

Stanton, S. 2006. The differential effects of dwarf mistletoe infection and broom abundance on the radial growth of managed ponderosa pine. For. Ecol. Manag. **223**(1–3): 318–326. doi:10.1016/j.foreco.2005.11.011.

Stanton, S. 2007. Effects of Dwarf Mistletoe on Climate Response of Mature Ponderosa Pine Trees. Tree-Ring Res. **63**(2): 69–80. doi:10.3959/1536-1098-63.2.69.

Stokes, M.A., and Smiley, T.L. 1968. An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago, IL.

Taylor, S.W., Carroll, A.L., Alfaro, R.I., and Safranyik, L. 2006. Forest, climate and mountain pine beetle outbreak dynamics in Western Canada. *Edited by*L. Safranyik and B. Wilson. Canadian Forest Service, Victoria, Canada.

Tocher, R.D., Gustafson, S.W., and Knutson, D.M. 1984. Water metabolism and seedling photosynthesis in dwarf mistletoes. In: Biology of Dwarf Mistletoes: Proceedings of the Symposium. Gen. Tech. Rep., U.S.D.A Forest Service.

Toms, J.D., and Lesperance, M.L. 2003. Piecewise Regression: A Tool for Identifying Ecological Thresholds. Ecology **84**(8): 2034–2041. doi:10.1890/02-0472.

University of Saskatchewan. 2006. Ecoregions of Saskatchewan. Available from http://www.usask.ca/biology/rareplants_sk/root/htm/en/researcher/4_ecoreg.php [accessed 15 September 2016].

Volney, W.J.A. 1998. Ten-year tree mortality following a jack pine budworm outbreak in Saskatchewan. Can. J. For. Res. **28**(12): 1784–1793. doi:10.1139/x98-147.

Volney, W.J.A., and Fleming, R.A. 2000. Climate change and impacts of boreal forest insects. Agric. Ecosyst. Environ. **82**(1–3): 283–294. doi:10.1016/S0167-8809(00)00232-2.

VoorTech. 2014. The Tree Ring Measuring Project J2X. VoorTech Consulting. Available from http://www.voortech.com/projectj2x/ [accessed 26 February 2016].

Weed, A.S., Ayres, M.P., and Hicke, J.A. 2013. Consequences of climate change for biotic disturbances in North American forests. Ecol. Monogr. **83**(4): 441–470. doi:10.1890/13-0160.1.

Wigley, T.M.L., Briffa, K.R., and Jones, P.D. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Climatol. Appl. Meteorol. **23**: 201–213.

Williams, P.A., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M., and McDowell, N.G. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nat. Clim. Change **3**(3): 292–297. doi:10.1038/nclimate1693.

Zang, C., and Biondi, F. 2012. Dendroclimatic calibration in R: The bootRes package for response and correlation function analysis. Dendrochronologia. doi:10.1016/j.dendro.2012.08.001.

Zha, T., Barr, A.G., van der Kamp, G., Black, T.A., McCaughey, J.H., and Flanagan, L.B. 2010. Interannual variation of evapotranspiration from forest and grassland ecosystems in western Canada in relation to drought. Agric. For. Meteorol. **150**(11): 1476–1484. doi:10.1016/j.agrformet.2010.08.003.

Zimmerman, G.T., and Laven, R.D. 1984. Ecological interrelationships of dwarf mistletoe and fire in lodgepole pine forest In: Biology of Dwarf Mistletoes: Proceedings of the Symposium. Gen. Tech. Rep., U.S.D.A Forest Service, Rocky Mountain Forest nd Range Experiment Station, Fort Collins, CO.

APPENDIX A: CLIMATE CORRELATIONS (1954-2014)

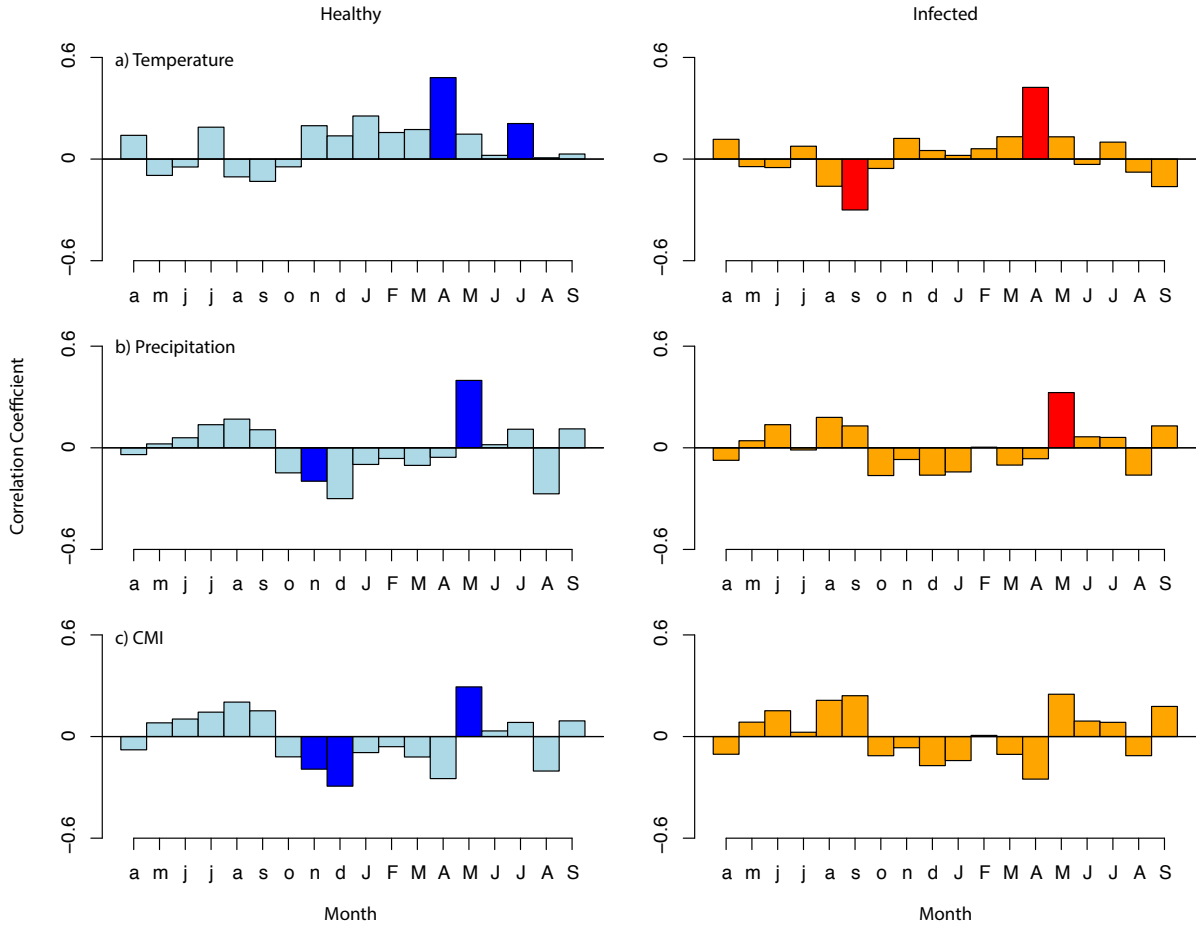

Figure A1: Northern region bootstrapped correlations (1954-2014) between residual master chronologies of healthy (blue) and infected (orange) trees and climate variables for the Northern region, from 1954-2014. The 18-month period was examined from April of the previous year to September of the current year. Lower case letters denote months of the previous year, and upper case letters denote the current year's months. The darker bars are significant at the 95% confidence level.

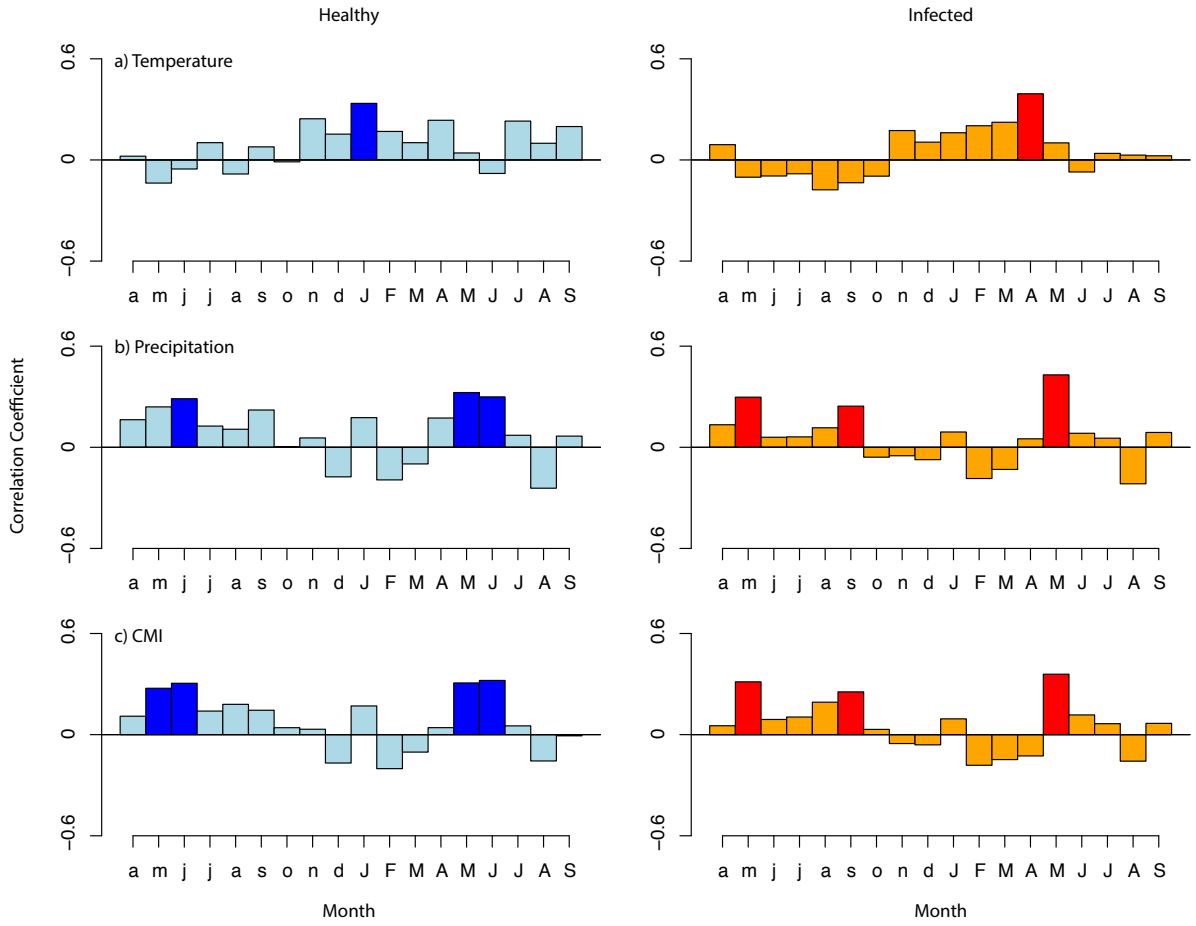

Figure A2: BERMS region bootstrapped correlations (1954-2014) between residual master chronologies of healthy (blue) and infected (orange) trees and climate variables for the BERMS region, from 1954-2014. The 18-month period was examined from April of the previous year to September of the current year. Lower case letters denote months of the previous year, and upper case letters denote the current year's months. The darker bars are significant at the 95% confidence level.

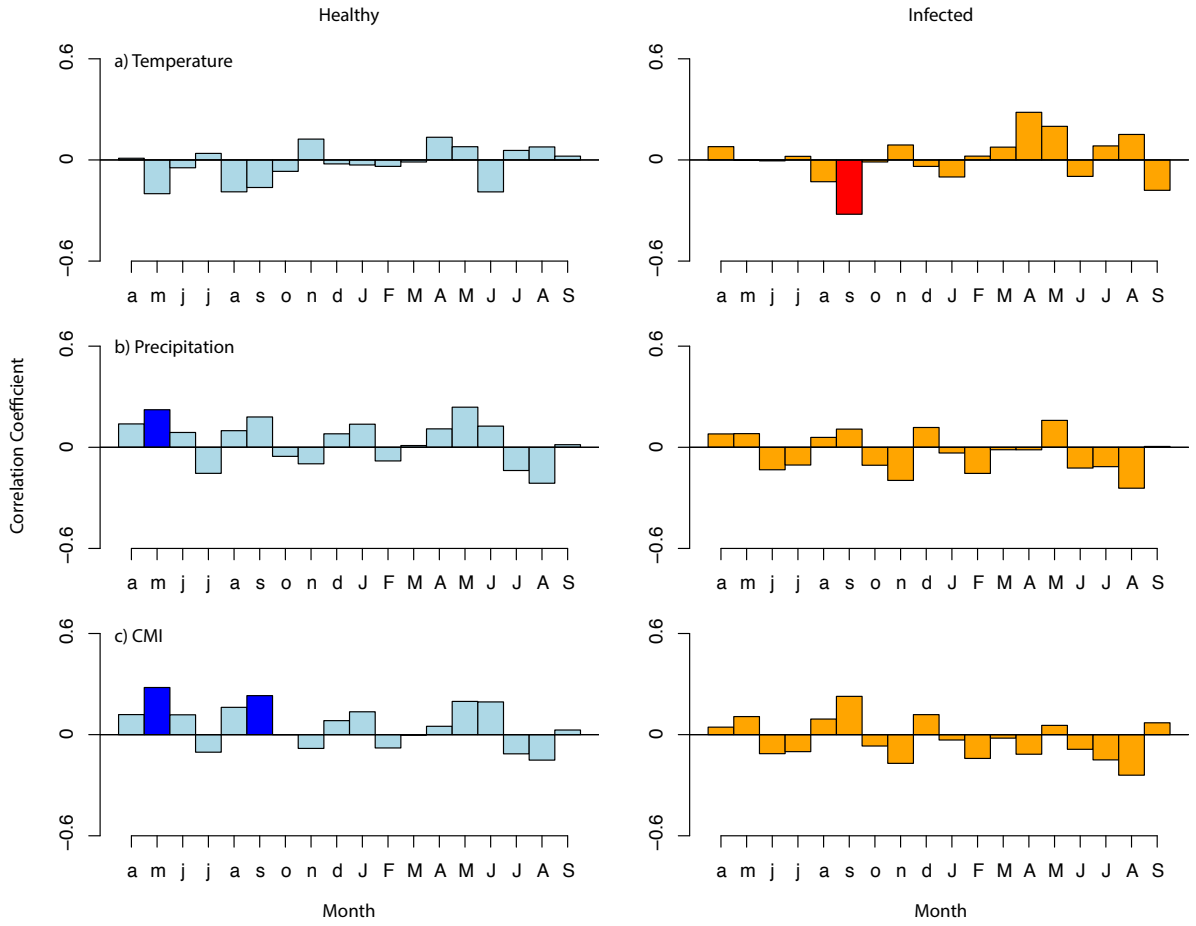

Figure A3: Southern region bootstrapped correlations (1954-2014) between residual master chronologies of healthy (blue) and infected (orange) trees and climate variables. The 18-month period was examined from April of the previous year to September of the current year. Lower case letters denote months of the previous year, and upper case letters denote the current year's months. The darker bars are significant at the 95% confidence level.

APPENDIX B: BROKEN STICK MODEL

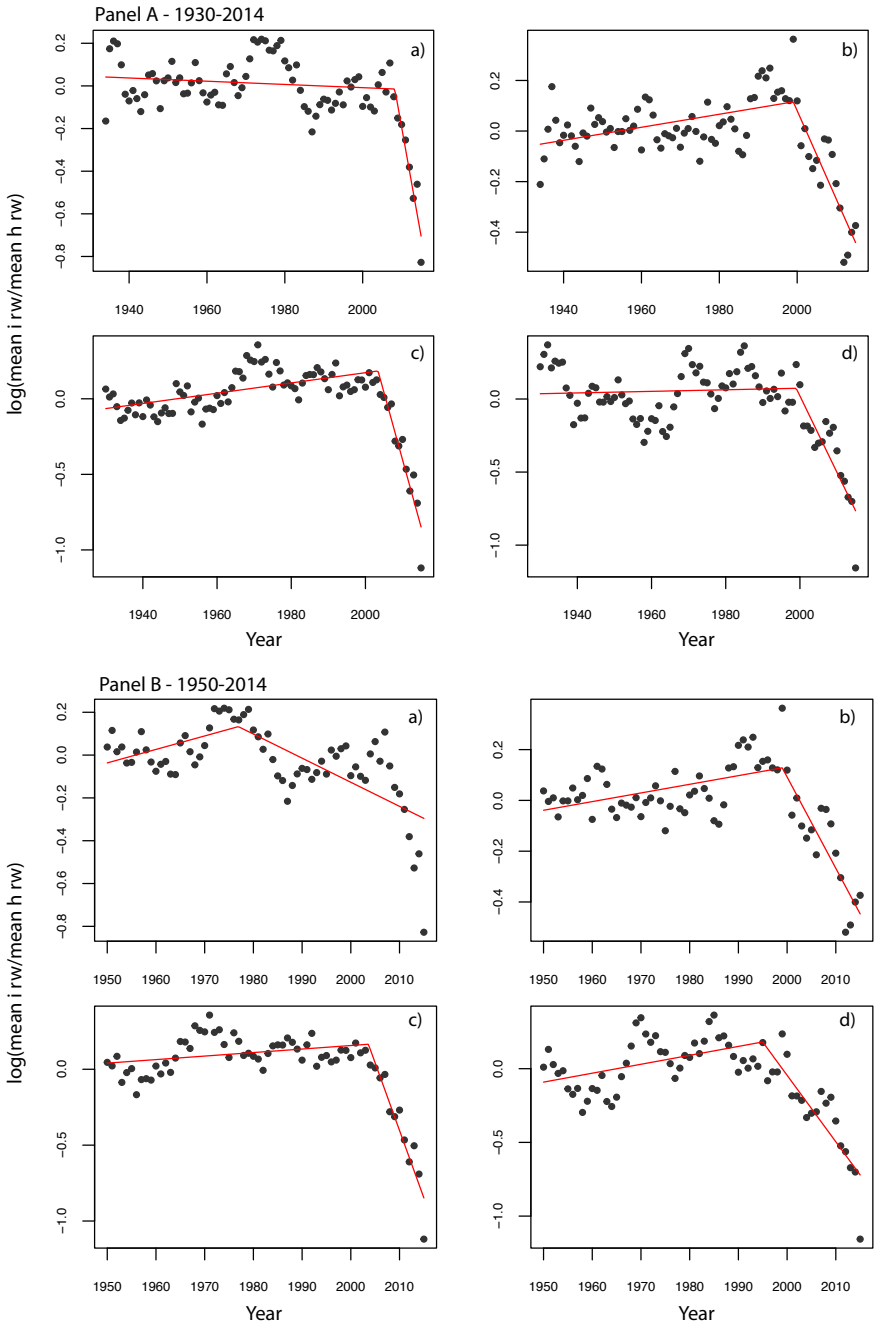

Figure B1: Change point detection in the Northern region using piecewise linear regression analysis. The x-axis is the time in years, and the y-axis is the log ratio (infected/healthy) of mean ring width. The red line shows the change in slope before and after the year detected as the change point. Panel A illustrates the results for the 1930-2014 time period (common interval); and panel B shows the results for the 1950-2014 time period for each site type (a) NI/NH; (b) NM1i/NM1h; (c) NM2i/NM2h; (d) NM3i/NM3h.

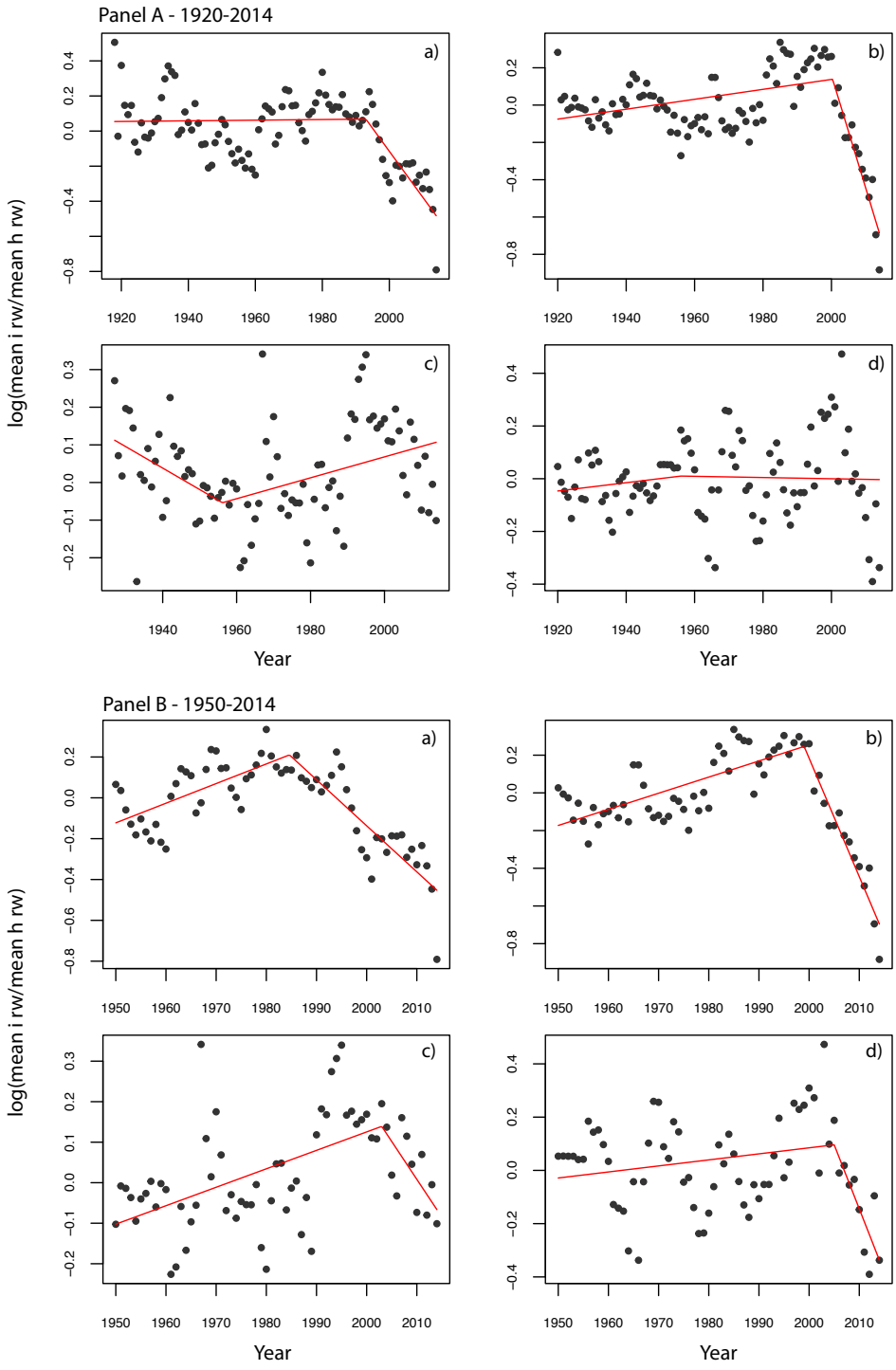

Figure B2: Change point detection in the BERMS region using piecewise linear regression analysis. The x-axis is the time in years, and the y-axis is the log ratio (infected/healthy) of mean ring width. The red line shows the change in slope before and after the year detected as the change point. Panel A illustrates the results for the 1930-2014 time period (common interval); and panel B shows the results for the 1950-2014 time period for each site type (a) BI/BH; (b) BM1i/BM1h; (c) BM4i/BM4h; (d) BM5i/BM5h.

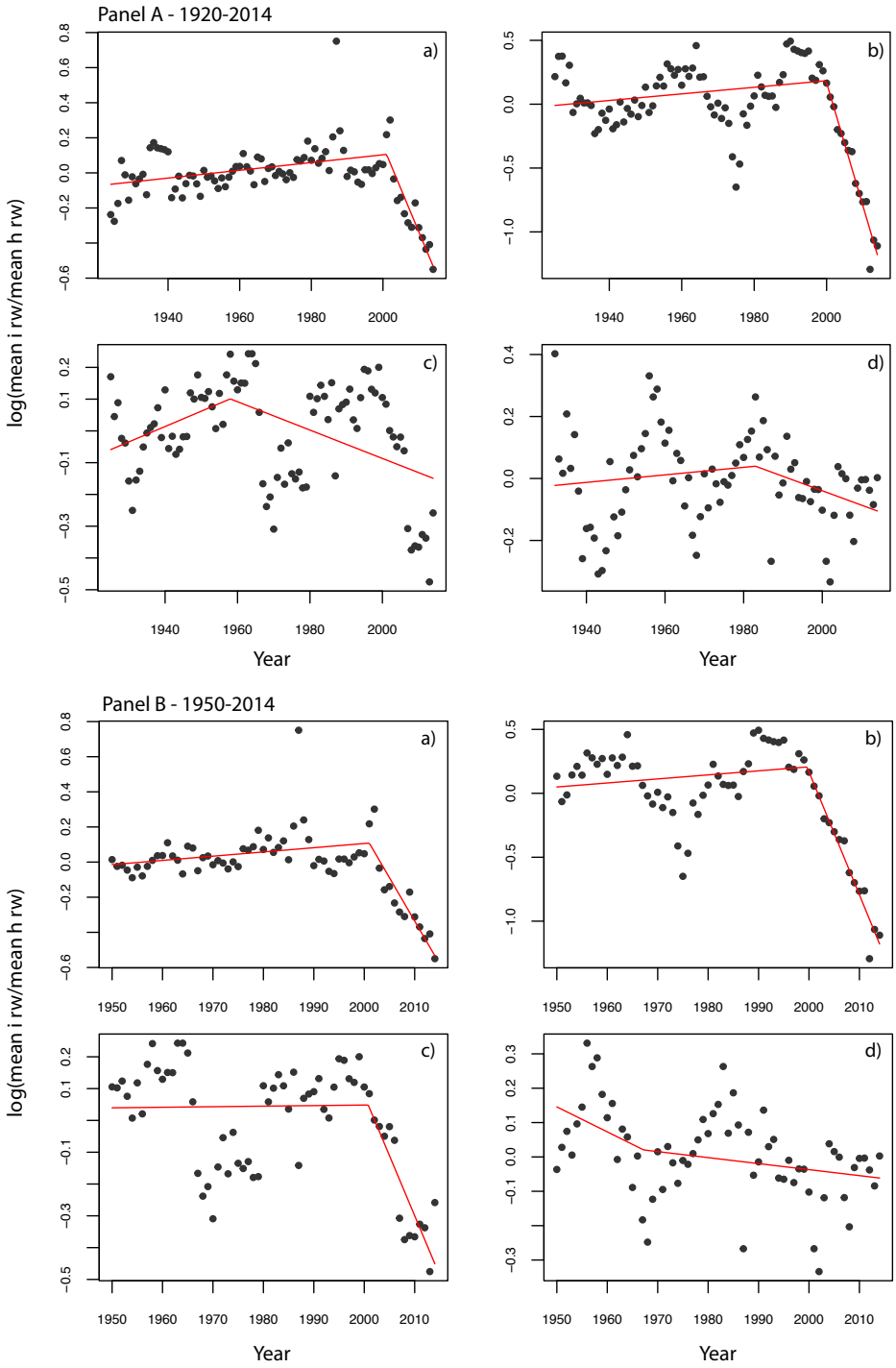

Figure B3: Change point detection in the Southern region using piecewise linear regression analysis. The x-axis is the time in years, and the y-axis is the log ratio (infected/healthy) of mean ring width. The red line shows the change in slope before and after the year detected as the change point. Panel A illustrates the results for the 1930-2014 time period (common interval); and panel B shows the results for the 1950-2014 time period for each site type (a) SI/SH; (b) SM1i/SM1h; (c) SM2i/SM2h; (d) SM3i/SM3h.